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VARIATION AND HYBRIDIZATION IN JUNIPERUS*

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INTRODUCTION

What prompted me to make population studies in *Juniperus*? As a Ranger in the National Park Service, prior to World War II, I was stationed in Platt National Park, Oklahoma, the home of a hybrid swarm between *Juniperus Ashei* Buchholz (called *Juniperus mexicana* Spreng., in 'Gray's Manual of Botany,' 8th ed. 1950) and *J. virginiana* L. Quite naturally, the junipers of the Park proved difficult to classify, and when I began graduate work after the war I found that botanists disagreed as to the identification of junipers in central Oklahoma. The study was begun because of the recognition of so many variants and intermediates between *Juniperus Ashei* and *J. virginiana*, but I had no idea of the extent of the problem until I drove to St. Louis in 1947. Along the way the same variations which I had known in Oklahoma and Texas were seen, again and again, on the knobs, glades, and cliff edges of the Ozarks. I wanted to find out just how extensive was the influence of the two species upon one another.

For such a study the correlation of several morphologic characters throughout the range of the species was chosen as the simplest and most direct means of showing how the plants were varying. This study is one in natural history, based on living plants and mass collections. Evidence of affinity, or lack of it, is circumstantial, not experimental; thus, theories and conclusions must be presented with considerable caution. I have attempted to explain the data in terms of the simplest hypotheses, keeping in mind their correspondences with similar data for other organisms which have been more intensively studied.

There are certain disadvantages in studying variation and evolution in a genus like *Juniperus*. Genetic data such as rate and direction of gene mutation or linkage patterns of multiple factor characters have not been obtained; the cytological

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data are meager since little more than a few chromosome numbers are known; the taxonomy awaits population studies for a suitable clarification; and the morphology is really well known for only two species. It is not a convenient group with which to do experimental work such as transplant studies (although widely distributed horticultural varieties may serve as a rough equivalent of transplant material). Students of evolution know that organisms which are well known in a general way are the best material for the study of the forces responsible for the development of discontinuities; whether they are discontinuities between individuals, populations, or higher categories (subspecies, species, or genera), but there are few such organisms. Enough facts have been documented for birds (Lack, 1947; Mayr, 1944) and insects (Kinsey, 1930, 1936, 1937) to give them significant usefulness in studies of speciation. A few plant species, such as those of the genus *Crepis* (Babcock, 1942, 1947), stand as beacons to what is yet to come from thorough studies of many other plants. We know from the many facts obtained from those organisms already analyzed that evolutionary processes are many and variable.

There are certain advantages in studying *Juniperus*. The genus is pragmatically suited to the multiple-correlate type of analysis for several reasons. For population analyses one needs populations. For many organisms these are either uncommon or difficult to find. Junipers characteristically grow in groups of marked prominence in the landscape. Generally, the plants occur in the open and are easily collected. Any one who has stood on an Ozark ridge in winter and looked across an area of old fields, knobs, glades, and cliff edges will appreciate the ease with which populations of *Juniperus* can be found.

The wide use of *Juniperus* as horticultural material is a great advantage in population studies. Individual trees and bushes, horticulturally superior, have been propagated asexually and have been widely grown in parks and gardens. The nurseries of D. Hill & Son (Kumlein, 1939), in particular, have named and propagated various clones. These include well-known horticultural varieties of *Juniperus virginiana*—"Canaertii", "glauca", "pyramidalis", and "pyramidiformia Hilli"; and of *Juniperus scopulorum*—"Moonlight", "Silver Juniper", "Blue Moon", "North Star", "Silver Glow", and "Hill Weeping Juniper". These serve as a rough but effective substitute for transplant experiments, demonstrating what proportions of plant-to-plant differences are caused by environmental influence and what by inherent qualities. Some of these varieties have been widely distributed in many different environments. Usually, they have been propagated vegetatively by grafting, but some have been grown from seed.

Juniperus virginiana var. *Canaertii* is one of those widespread cultigens which makes possible a study of the morphological effects of varied environments. It is a picturesque variety with long, well-separated branches and irregular masses of compact dark-green foliage, and it bears fruit profusely every second or third year. It is propagated by grafting, usually onto a native Red Cedar root system. Three populations of this clonal variety were studied, one in Oklahoma, one in Missouri, and one in Michigan. These data are discussed under "Study of Variation."

In recent years the shelter-belt plantings, carried out under the supervision of the Soil Conservation Service, have consisted of woody plants which could stand the rigorous climate of the great prairie and high plains. *Juniperus* has figured heavily in this development. Farmers from the western Oklahoma wheat belt have noticed the variation in the junipers used for shelter-belt plantings there and some have inquired about it. Three "species" are generally being used: *Juniperus Ashei*, *J. virginiana* (and hybrids), and *J. scopulorum*. In the future one may see small hybrid swarms scattered about farm buildings and shelter-belts in the Midwest and Southwest. One can easily see the value of these plants, especially of the hybrids, in these situations. In such rigorous climates as the high plains, a little of the germ-plasm of *J. scopulorum* coming in from slightly higher altitude to mix with *J. virginiana* produces a plant well adapted to existence on the Llano Estacado. Also, a little of the *Juniperus Ashei* germ-plasm in *J. virginiana* produces a plant which may stand the rigors of western Oklahoma, Kansas, Nebraska, and similar areas where other trees exist on the uplands only with the greatest difficulty.

The general method of studying variation in *Juniperus* is based on Anderson's (1949) "corollary of the demonstration of multiple factor linkage." When germ-plasms are mixed, linkages are a strong barrier to the recombinations of multiple-factor characters. Since the multiple-factor characters generally tend to stay together, the variation patterns in a mixed population tend to fall into three categories: those resembling the one parent, those more or less intermediate, and those resembling the other parent. There may be considerable recombinations and resultant variation, but the degree of both must depend first on the extent to which linkages can be broken.

The term "introgression" was applied by Anderson and Hubricht (1938) to the gradual transfer of genes from one species to another as a result of hybridization (involving repeated back-crossing) at the juncture of the distributions of the hybridizing elements. If introgression is occurring in *Juniperus*, it should be evident in several ways: (1) there should be some kind of evidence that, given the opportunity, the species in question will hybridize; (2) there should be evidence of recombinations of the characters from the two species; (3) the presence of the characters of one species in the other species should be in progressively greater dilutions away from the region of hybrid swarms; and (4), most significantly, the characters which differentiate the two species should be at least slightly correlated throughout the area of introgression.

An analysis of introgression is simplified if the organisms introgressing are very different. *Juniperus Ashei* and *J. virginiana* are easy to analyze since they differ widely in morphology and in ecological preference. As will be shown subsequently, their differences in growth form and in all the classical technical characters used in differentiating species of *Juniperus* are outstanding.

THE SPECIES

Juniperus is the third largest genus in the Coniferales and is probably as prominent in the extent of its distribution. It contains approximately forty species though over sixty have been described. The genus has achieved complete northern hemispheric distribution which is a fact undoubtedly related to the value of the berry-cone as a food for birds. It seems to be one of the more youthful genera of the Coniferales since it probably evolved from a transition Cupressoid probably not later than the Cretaceous. Specimens of Upper Cretaceous *Juniperus* have been reported from New England by Hollick (1902) and Berry (1906). Upper Cretaceous fossils of *Juniperus* have been reported from Greenland (Darrah, 1939) which are similar to the modern members of the OXYCEDRUS section. These types were apparently part of the so-called Arctotertiary flora. In America, fossils of the SABINA section of *Juniperus* are known from the Pliocene—the Weiser flora (Dorf, 1938), a transition flora in the Payette formation of southwestern Idaho, contains one species of *Juniperus* apparently the counterpart of modern *J. occidentalis*. From the Pleistocene, specimens of *J. virginiana* have been found in the Don Valley (Berry, 1910; Penhallow, 1907), and specimens of *J. californica* have been reported from the Rancho La Brea tar pits near Los Angeles (Mason, 1927).

The modern xerophytes of the genus have evidently evolved with the development of our modern deserts, apparently during the late Cenozoic, probably since the Miocene. The junipers may have arisen from a transition Cupressoid inhabiting warm temperate regions characterized by winter rains and prolonged summer droughts. The seemingly most primitive species, *J. drupacea* and *J. oxycedrus*, are characteristic plants of what Schimper (1865) has called the sclerophyllous woodlands of the North Temperate Zone. The majority of the species, the appressed scale-leaved ones, are characteristically found in semi-arid regions or in arid regions at mid-altitudes (where microthermal conditions prevail). Exceptions to this climatic generalization are *J. virginiana* and *J. barbadensis*, which occur in sub-humid or humid climates and may attain great size, the former tending to occupy the least mesic habitats.

On each continent most of the species are centered about the Pacific side and are nearly equally divided between Eurasia and America. The present distribution of abundance of species in *Juniperus* is best explained by Buchholz' (1948) idea, that the Pacific perimeter probably represents the distribution center of the Coniferales during their most recent speciation cycle.

Endlicher (1847) created three sections in the genus *Juniperus*: CARYOCEDRUS, OXYCEDRUS, and SABINA. These sections constitute an interesting transition series, especially with regard to the female cones and the leaf types. The transitions are from partly woody somewhat cupressoid-like cones in section CARYOCEDRUS to completely fleshy berry-cones in section OXYCEDRUS, and from the acicular-type leaves to reduced scale-type leaves in section SABINA.

The single species in the section CARYOCEDRUS, *Juniperus drupacea*, may represent a relatively unsuccessful attempt at evolution toward a woody-coned form in this predominantly sclerophyllous and xeromorphic genus, or it may represent the sole surviving species of a more ancient group of junipers. This species is confined to the eastern part of the Mediterranean region.

There are approximately ten species in the section OXYCEDRUS, one of which, *Juniperus communis*, is circumboreal. Seven species are found in eastern Asia (China, Japan, Korea), a Pacific perimeter distribution, and two have a Mediterranean coastal distribution but extending through Persia to the Caucasus. The species of this section are characterized by acicular leaves as in CARYOCEDRUS, but they have fleshy berry-cones which are usually close to a centimeter in diameter, intermediate between the twice larger cones of CARYOCEDRUS and the generally small ones of SABINA.

The SABINA section is much the largest, containing approximately thirty species. The majority of these are found in the more mesic habitats within and at the edges of the North American deserts. In the Old World about ten species are found from the Mediterranean to the Himalayas, China, and Japan.

Subdivision of the sections becomes a rather arbitrary matter since the constituent species are all relatively similar morphologically. However, one character is available which clearly separates the species of the SABINA section into two groups. This character is the presence or absence of teeth-like processes on the margins of the leaf—single cells which project out from the other marginal cells at uniform intervals. The more mesic species, *Juniperus barbadensis*, *J. virginiana*, *J. scopulorum*, *J. horizontalis*, and *J. Sabina*, have entire margins while the more xeric ones, *J. californica*, *P. pachyphloea*, *J. occidentalis*, *J. monosperma*, *J. Pinchoti*, and *J. Ashei*, make a well-marked series from *californica* with very large teeth, to *Ashei* with relatively small ones.

The species discussed in this study include five of those which occur east of the Rocky Mountains. One of these (*Juniperus Ashei*) is a member of the species group with denticulately fringed leaf margins, while the other four (*barbadensis*, *virginiana*, *horizontalis*, and *scopulorum*) are generally more mesic and are in the species group with entire leaf margins. Population studies have been made for three of them in regions where each meets *Juniperus virginiana*. Fassett (1944-'45) made studies of populations showing introgression between *J. scopulorum* and *J. virginiana*. The data for *Ashei* and *virginiana* are presented in this paper.

A key to all native species of the SABINA section adjacent to or overlapping the range of *Juniperus Ashei* and *J. virginiana* follows. It was made up from the examination of many specimens, and yet it combines elements of keys from Rehder (1940), Fassett (1945), and Hall (1947).

This key is not constructed for the purpose of differentiating every variant, whether sport or hybrid, but expresses the fundamental differences between the species. For example, *Juniperus virginiana* L. var. *ambigens* Fassett is a trailing to semi-upright shrub generally with the habit of *J. horizontalis* but with the tech-

- A. Leaves* with denticulately fringed margins.
1. Mature fruit** red or coppery; glands on leaves round, usually ruptured..... 1. *J. Pinchoti*
 1. Mature fruit blue or blue-black.
 2. Leaves glandular; glands elliptic and flat on all leaves; seed light chestnut-brown..... 2. *J. monosperma*
 2. Most of the leaves eglandular; glands, when present, round and swollen, especially on the old leaves; seed dark chestnut-brown.... 3. *J. Ashei*
- A. Leaves with entire margins.
3. Leaves overlapping, tips acute; glands oval or rarely elliptic and shorter than the distance from the gland to the leaf tip.
 4. Creeping shrub; fruit bluish, 6.5–8 mm. in diameter..... 4. *J. horizontalis*
 4. Upright tree; fruit blue-black, less than 6.5 mm. in diameter.
 5. Leaves less than 2 mm. long; fruit 3–4 mm. in diameter, wider than long..... 5. *J. barbadensis*
 5. Leaves 3–4 mm. long; fruit 3.5–6 mm. in diameter, very slightly longer than wide..... 6. *J. virginiana*
 3. Leaves not overlapping, tips obtuse; glands elliptic or rarely oval and longer than the distance from the gland to the leaf tip..... 7. *J. scopulorum*

*Leaves in the key refer only to the mature scale leaves.

**Fruit measurements refer to mature material during its current season, and are made across the fruit, not lengthwise.

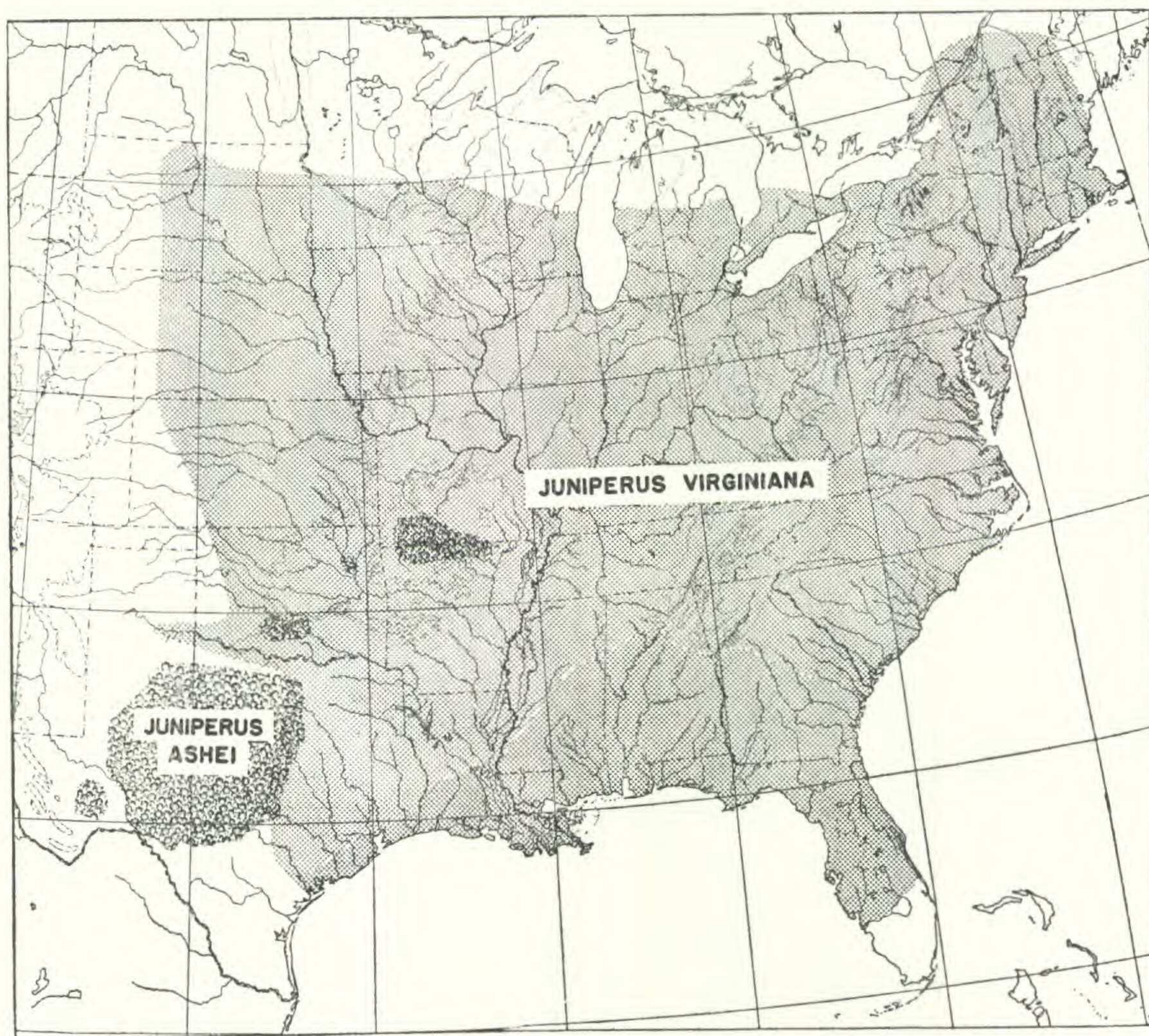
nical characters of *virginiana*. Such names as *Juniperus virginiana prostrata*, *J. Sabina procumbens*, *J. virginiana* var. *reptans*, *J. virginiana horizontalis*, *J. virginiana* var. *Kastenii*, and *J. virginiana Kosteri*, which appear in horticultural literature or on herbarium specimens originating from the coast of Maine, are to be referred to *Juniperus virginiana* L. var. *ambigens* Fassett (supposedly a variety of hybrid origin). The same situation holds for *Juniperus scopulorum* var. *patens* Fassett, which is a procumbent plant with the habit of *J. horizontalis* and with most of the technical characters of *J. scopulorum*. Fassett considers it as a probable hybrid between the two species.

The taxonomy of the genus is in great confusion for several reasons. First, some of the early botanists made specimens of juvenile or mixed foliage and later described these as new species when actually they represent growth-stage differences within one species. Some of the specimens to which Linnaeus (1753) gave new names were juvenile or mixed-foliaged material. Second, poorly selected material by the collectors usually led to descriptions and illustrations which, particularly before the time of Engelmann, were not adequate to differentiate newly described species from species previously established. Engelmann's (1877) short paper on the American SABINA section is the classic in the taxonomy of the genus. He apparently understood junipers better than any of his contemporaries. Third, once an error became established (published), it tended to be perpetuated. Thus, errors in supposed distribution caused errors in the reference of collected material to species where actual study of comparative morphology was not carried out. Fourth, mistakes are easy to make with junipers, partly because the measurable characters are relatively so small. The leaves are small; the glands are small (near the limit of unaided visibility); the leaf margin differences are almost microscopic; the sporophylls and other structures of the staminate cone and young ovulate cone are likewise minute. There are several large areas of intergradation

between species of *Juniperus* in the United States alone, presumably the result of hybridization. It is well known that extensive hybridization may make a group of organisms difficult to classify. In long-lived plants with efficient dispersal mechanisms, even a small amount of hybridization may be sufficient to make a group somewhat chaotic in its morphologic character patterns. Such plants may give rise to partially hybrid progeny year after year; and many of these progeny may find a hold in nature, especially if they are organisms which are adapted to disturbed environments.

DISTRIBUTION OF THE TWO SPECIES

The distribution limits of *Juniperus Ashei* and *J. virginiana* are shown in Map I. The method of mapping does not convey a concept of density of distribution, and the density is anything but uniform. Several factors are responsible for variations in the number and spacing of individuals in stands, some of which are discussed under "Population Structure." Both species are probably more abundant now than in the last century because of the cessation of fires and the greater area of



Map 1. Showing distribution of *Juniperus Ashei* and *J. virginiana*.

bare ground as a consequence of the misuse of land. At the same time, there are fewer large plants, since both species have numerous economic properties. The larger specimens of Red Cedar in the South have practically disappeared.

Juniperus Ashei has a disjunct distribution. It forms dense "brakes" which literally cover the Edwards Plateau in Texas, mostly the area represented by the Comanche Series of the Cretaceous, from the Pecos River to Howard County to Palo Pinto County and south along the base of the Balcones Escarpment. Outlying specimens have been reported from Brewster and Terrell counties in southwest Texas, in Garza County along Double Mountain Fork, in Baylor County along the Wichita River, and in Wise County. A gap of nearly 100 miles occurs between populations from the northernmost distribution in Texas and the Arbuckle Mountains in Murray County, Oklahoma. In the Arbuckles it is found on non-dolomitic limestones which form fairly deep, well-drained soils with relatively high water-holding capacity. The only other stands occurring in Oklahoma are found nearly 200 miles northeast of the Arbuckles along the bluffs of Pryor Creek near Grand River. The northernmost outposts of Ashe Juniper are the bluffs and bald knobs of the White River in northern Arkansas and in southern Missouri as far east as McVey Knob in Ozark County. The easternmost known naturally occurring *Juniperus Ashei* is on the bluffs of the South Fork Spring River in Randolph County, Arkansas. There are four specimens planted at the Missouri Botanical Garden Arboretum, Gray Summit. Three are from southwestern Missouri, and one from the Arbuckle Mountains, Oklahoma. Whether this species grows in Mexico is not definitely known. It is possible that it might be found across the Rio Grande from Val Verde County. However, Martinez (1946) expressed doubts as to its presence south of the Rio Grande.

In the western portion of its range, *Juniperus Ashei* hybridizes (as judged from morphological criteria) with *J. monosperma* and *J. Pinchoti*. Hybrids between *J. Ashei* and *J. monosperma* have been collected in Texas near Marathon, Brewster County, and at numerous places in Terrell County. Hybrids between *Ashei* and *Pinchoti* have been collected near Comstock, Val Verde County, in northern Kimble County, and along the North Concho River in Tom Green County. A line drawn from Del Rio, Val Verde County, northeast to Fort Worth, Tarrant County, would nearly separate *J. Ashei* from its hybrids with *J. Pinchoti* westward.

Juniperus virginiana ranges from southern Maine to southern Ontario to northern South Dakota to Texas and eastward to the Atlantic Coast. It is a complex species with many variations which show only loose trends. When the variants produced as a result of hybridization are included in the complex it becomes a most heterogeneous species. When Engelmann (1877) wrote that its range was exceptionally great, he was including *J. scopulorum* as identical with *J. virginiana*. However, he also remarked that no other conifer extends through so many degrees of latitude. If the West Indian Lax Juniper (*J. barbadensis*, *J. lucayana*, *J. silicicola*) is included as a variety of *J. virginiana*, as some authors have insisted, then Engel-

mann's latter remark takes on added significance. However, typical specimens of *J. virginiana* and *J. barbadensis* Sarg. are quite as different as many other species in the genus, even though introgression has apparently tended to submerge these differences to the casual observer.

ECOLOGY

The ecological story portrayed by the two species is most interesting. *Juniperus Ashei* has rather definite requirements for growth and reproduction, but *J. virginiana* will survive under a very wide range of conditions. The distributions of these species clearly point out the possibility for differences in tolerance to environment. Since all members of the SABINA section require the same basic conditions, in somewhat varying degrees, for establishment (some bare ground or at least thin cover, good drainage, and a high pH), it seems reasonable to assume that, where chances are equal, the absence of one species may be by reason of inherent physiological factors.

The following table furnishes a crude illustration of the relations between the presence of *Juniperus Ashei* and soil type (in all cases calcareous), precipitation, and temperature.

	Av. Ann. Temp. (40 yr.)	Av. Ann. Precip. (40 yr.)	Substrata
Ozark Mts.	56° F.	45 inches	Dolomite (thin soil) knobs and glades
Mayes Co. Okla.	60° F.	40 inches	Non-dolomitic limestone cliffs (no subsoil, rapid drainage)
Arbuckle Mts.	63° F.	36 inches	Non-dolomitic limestone knobs (occur here only on relatively horizontal strata)
Edwards Plateau	65° F.	20–30 inches	Non-dolomitic limestone, massive, porous, cavernous, (on horizontal strata)

As the precipitation effectiveness decreases from the Ozarks to central Texas, the soil factors improve somewhat. The plants will grow on very thin soil (4–6 inches to bed-rock on glades) or on very rocky sparsely covered knobs where the soil type is classified as rough, stony land.

Juniperus Ashei, while quite restricted in its range, produces great quantities of large, palatable berries which are consumed by birds and small mammals. This species has a slight advantage over *J. virginiana* in the production of fruit. In the bald knobs of southwestern Missouri the two species occur together, with their hybrids in relatively equal numbers; but the regions surrounding the knobs are covered with the introgressants toward *J. virginiana* in all age stages, while the most xeric portions of the knobs, the southwest slopes, or a cliff in the vicinity,

are covered with specimens which show the recombinations of characters closest to *J. Ashei*. In the Missouri knob country, the most *Ashei*-like plants always grow on shallow soils containing a high proportion of magnesium carbonates (a dolomite-derived soil). This is the most xeric environment of the region, and this is shown in the structure of the rest of the flora. The knobs and glades support a thin prairie-type flora with many species characteristic of the Southwest. *Andropogon scoparius* and *Bouteloua curtipendula* are common, with some of the bare spaces more or less covered by *Sporobolus ozarkanus*. From this basic cover spring such southwestern plants as *Palafoxia callosa*, *Centaurium texense*, *Yucca glauca* var. *mollis*, *Baptisia minor*, *Astragalus mexicanus* var. *trichocalyx*, *Cotinus obovatus*, *Juniperus Ashei*, *Petalostemum pulcherrimum*, and *Rudbeckia missouriensis*, along with the more widely distributed plants of barrens and prairie-openings such as *Agave virginica*, *Isoetes Butleri*, *Ophioglossum Engelmanni*, *Psoralea esculenta*, *Lobelia spicata* var. *leptostachys*, *Echinacea pallida*, *Coreopsis grandiflora*, and others. The most common woody plants, other than juniper, are *Ulmus alata*, *Bumelia lanuginosa*, *Cercis canadensis*, *Rhus aromatica*, and *Fraxinus quadrangulata*. Detailed studies of Ozark glades have been made by Brenner (1942) and Erickson, Brenner and Wraight (1942).

The prairie-openings of the Ozarks are like little pieces of the Southwest transferred intact into the Ozark forest region. Floristically and edaphically these knobs and glades are southwestern, yet these open spots are scattered and disjunct. Whole floras cannot migrate inadvertently, but the evidence is overwhelming that the Ozark region extending southwestward into Oklahoma was once much more open and that the ridges and steep upland slopes were eastward extensions of the prairie flora. The facts concerning the migration of whole floras during and following glaciation are being knit together. Pollen analysis is the master key to the late Pleistocene structure of vegetation in glacial and in periglacial regions. Changes in the landscape which have occurred in the last hundred years or so may be inferred from county records and surveyor's notes, from travel notes (e.g. Josiah Gregg's letters, ed. Fulton, 1941, 1944), from Army-sponsored explorations and surveys (e.g. Marcy, 1866; and House of Rep. Ex. Doc., reports on explorations and surveys), from Geological Survey reports, and from many other source works. Suffice it to say that changes in vegetation structure are not only characteristic of past ages but are going on today. A good review of these vegetational changes has been given by Beilmann and Brenner (1951).

In the Arbuckle Mountains of south-central Oklahoma, *Juniperus Ashei* is much more abundant than *J. virginiana*. However, this hilly island of *J. Ashei* is practically surrounded by rather dense local populations of *J. virginiana*. Directly west of the Arbuckles, Red Cedar is not abundant until, beyond the belt of Post-Oak, Black-Jack savannah, it is found on the ridges and hills of the western Oklahoma prairies. The most extensive and dense populations of *J. virginiana* in Oklahoma are found, as in Missouri and Texas, in prairie environments in early stages of succession, in disturbed prairie areas, or in prairie-openings in the savannah and oak-hickory forest.

The Arbuckle Mountain region is classified (for convenience) by Bruner (1931) as Post-Oak, Black-Jack savannah in a prairie climate, even though the vegetation units constitute a complex series of edaphic variants. In regions of critical climate, where climax formations are in transition, external factors such as lithological character, topography, and soil moisture may strongly affect the distribution of the transition vegetation to produce marked zonations (see Warner, 1926). The limestone areas of the Arbuckles show floristic affinities with the Ozark knobs and glades and the Edwards Plateau, even though they are disjunct from both. The Arbuckles constitute a plateau of about 860 square miles rising a few hundred feet above the surrounding prairie with a west-to-east slope from 1,350 feet to 750 feet. This plateau shows a definite mountainous structure with much faulting and folding which have resulted in 12,000 feet of upturned strata giving an unbroken horizontal sequence of sedimentary deposits from Cambrian to Pennsylvanian time. The original mountains were uplifted in the Carboniferous, while the present aspect is the result of erosion which sliced off the synclinal and anticlinal features down to the mountain heart—leaving the differently eroded upturned strata. Cretaceous deposits from epicontinental seas were stripped from the region after late Cretaceous uplift, a consequence of the Laramide Revolution.

The Arbuckle Mountains, with hard-rock truncated anticlines and domes alternating with softer rock synclines and basins, is an outdoor laboratory wherein the effect of lithological factors on the structure of vegetation may be conveniently studied. Each stratum has its own characteristic soil or rough stony covering. Water relations in this region of low rainfall are consequently critical and varied. The line of demarcation between a grassland community on Arbuckle limestone and an oak-savannah community on Reagan sandstone is as fine as a knife-edge. The southwestern species listed above for the knobs and glades of the Ozarks likewise occur on these dry Oklahoma hills. The flora of the Arbuckles shares with that of the Edwards Plateau such plant species as *Juniperus Ashei*, *Carya Buckleyi*, *Quercus texana*, *Rhus copallina* var. *lanceolata*, *Cercis canadensis* var. *texensis*, *Abutilon incanum*, *Psoralea Reverchoni*, *Dalea frutescens*, *Lindheimera texana*, *Forestiera pubescens*, *Sophora affinis*, *Fraxinus texensis*, and *Juglans major*.

The occurrence of *Juniperus Ashei* alone in the Arbuckle area deserves an ecological analysis. The species is apparently restricted to two horizons—the Pontotoc conglomerate and the Viola limestone. With the exception of the dolomitic Arbuckle limestone where *Juniperus Ashei* does not occur, these two horizons are the most xeric in the area.

The term Edwards Plateau is used in the most popular sense to include the Comanche Plateau and the Edwards Plateau proper and is roughly the area from the Brazos River south and east to the limit of the Balcones Escarpment and west to the valley of the Pecos River (roughly the Comanchian biotic province, Dice, 1943). The massive Edwards limestone, which is responsible for a magnificent stratum plain in the southern half of the area, is porous, well-drained, and covered with a thin, rocky, chocolate-brown soil of a relatively low organic content.

The distribution of *Juniperus Ashei* a hundred years ago was not the same as it is today (Bray, 1906). In the last century, the Edwards Plateau supported a tall-grass prairie flora and woody vegetation consisting of such species as *Juniperus Ashei*, *Quercus virginiana*, *Q. Laceyi*, and *Q. texana* growing on the drier slopes of the much-dissected Balcones Escarpment, and the more mesophytic species in the valley bottoms, canyon floors, and along the flood-plains. As a result of the gradual cessation, or at least control, of fire and because of the thinning of the grass cover through overgrazing, the upland woody species have become established on the Edwards Plateau and in some areas form very dense thickets. Thus, *Juniperus Ashei* now occupies about 4,000,000 acres, probably four times its last-century areal distribution, and some stands are so dense that defoliation of the lower branches results. In the areas upon the plateau where *J. Ashei* has spread, it is associated with *Stillingia texana* except in the "brakes" where there is practically no understory. Competition for water is extremely great in these brakes. When precipitation is long in duration and gentle or when short in duration but rapid, the water does not percolate through the root systems of the junipers. Core drills show that most of this water is absorbed and transpired by the junipers. Both Ashe Juniper and Red Cedar have strong tap roots, but the former has very extensive lateral roots mostly in the surface foot of soil. A "brake" of *Juniperus Ashei* might be compared to a sod-forming grass, and, like the sod, it is relatively well closed to invasion. The increase in range of *Juniperus Ashei* is an important economic problem for the state of Texas, and the ranchmen of the Edwards Plateau are "bulldozing" junipers in order to get a return growth of grass.

The widely varying habitats of *Juniperus virginiana* throughout its range are an important factor in its hybridization. In the Interior Low Plateaus¹ where it is most homogeneous morphologically it is also relatively homogeneous in apparent ecological character. The two habitat types which may be recognized are the forest-clearing and old-field type, which may also be found occasionally on flood-plains, and the glade type, which is typified by the Red Cedar growing on the Lebanon limestone in the glades of the Nashville Basin. This glade type is the more xeric adaptation in the eastern type Red Cedar. The morphological variation between the two types is concordant. Both of these forms are predominantly calciphiles.

In the South along the coastal plain, *Juniperus virginiana* tends to grade into the small-fruited lax-foliaged *J. barbadensis*, which is native to the Florida peninsula and cultivated along the Gulf coastal plain. Sargent (1902) described *Juniperus barbadensis* as: "growing usually in inundated river-swamps and forming great thickets in forests of Taxodium, Red Maple, Gordonia, Loblolly Pine, Swamp Oaks, Palmetto, and Liquidambar." Red Cedar, the lax type, on the coastal plain (1-B² area of Map 3) also occurs in swamps, low wet woods, and along flood-plains. In the northern areas (1-H area of Map 3) it grows on sandy soils, dunes, and

¹The province (after Fenneman, 1938) called the Interior Low Plateaus is here referred to.

²"1-B" refers to the introgressants of *Juniperus virginiana* and *J. barbadensis* Sarg. Originally I was using the synonym, *J. lucayana*, hence "1-L" on Map 3.

shore lines, along with *Juniperus horizontalis*. Where limestone is present, it forms extensive stands. In the northwest area of its range (1-S area of Map 3), Red Cedar occurs chiefly on the river bluffs and along ridges. In recent years it has migrated into old fields and overgrazed pastures. In the Ozark region and southward, it occurs in a variety of habitats from wet flats to the most xeric knobs or cliff edges. It will be seen that, on the whole, habitat preferences are correlated with introgressing characters.

It is well known that elements of the northern coniferous forest have migrated far south, to Texas and Louisiana, in a pluvial period following the advance of the Wisconsin ice sheet. Pollen horizons (Tharp and Potzger, 1947; Potzger, 1946; Potter, 1947; Deevey, 1949, 1951) clearly indicate that the post Pleistocene vegetation in eastern United States has fluctuated, and correlates with trends in climatic change from cool moist (boreal conifers) to cool dry (pine and oak) to warm moist (beech and hemlock) to warm dry (oak-hickory and grasses) to cool moist. These periods have been named by Blytt (1882) as boreal (cool dry), Atlantic (warm moist), sub-boreal (warm dry), sub-Atlantic (cool moist), and the general theory behind these names became known as the "Blytt-Sernander hypothesis." The maximum of the xerothermic period, corresponding to Blytt's sub-boreal period, has been estimated to be 4,000 to 6,000 years ago.

Whatever may have been the effect of Tertiary or interglacial xerothermic periods on the migration of these southwestern species, it seems reasonable to assume that the present distribution of these elements was initiated by migrations since the recession of the Wisconsin ice sheet, and that these previously more widely distributed elements have since contracted in range to the confines of areas edaphically suitable. It is assumed that the southwestern element has thermic requirements which were satisfied by the sub-boreal and possibly the late-glacial periods.

Some recent work (Cain, 1948; Potzger, 1946) points to the probability that fluctuating xerothermy was the characteristic sub-boreal condition. The distribution of forest and prairie throughout that time expanded and contracted in a minor way, probably remaining fairly closely associated and probably not differing markedly from the modern pre-lumbering forest-prairie distribution. At any rate, the sub-boreal pollen diagrams are characterized by the dominance of oak species with a slight rise in *Carya* and *Pinus* and a fall in *Acer* and *Fagus*. The eastward extension of the prairie (the prairie-peninsula) probably occurred at that time. The southwestern element could have gradually become established in edaphic situations where it could compete with the more characteristic prairie species. The presence of *Juniperus Ashei* in the Ozarks is not hard to explain; however, the presence of the accompanying floristic elements cannot satisfactorily be explained as a fortuitous long-distance migration and establishment in competition with the adjacent prairie species. Also, the existence of habitat continuity is impossible to demonstrate either for recent times or for a xerothermic period.

The most plausible hypothesis, for which there is only a shred of evidence, to explain the presence of the southwestern element on Ozark knobs and glades is

that the migration and establishment occurred when the region was successionally primitive in the late-glacial period. Since the ice-lobes in the middle-western region stopped at so low a latitude, it is not wholly necessary to assume that the peri-glacial area was thoroughly cold, and it was certainly dry. Off-glacier winds mixing with the prevailing southwesterlies would repel and turn the southeast trades and push the storm track southeastward toward the Appalachians and the coastal plain. The peri-glacial area west of the Mississippi may have become colonized by southwestern and more typical tall-grass prairie species at about equal rates. Later, as the Wisconsin ice sheet receded, these southwestern and prairie communities migrated northward along the southern face, the coastal-plain element along the southeast face, and later Red Spruce migrated from the Appalachians north and westward (Cain, 1948). During the boreal and Atlantic periods, these southwestern and prairie floras may have been dissected and reduced by the great increase of the forests (the spruce-fir, pine, and later the oak-hickory). With the advent of the sub-boreal period, the restricted prairie floras may have expanded again, only again to contract to the present distribution.

Evidence of late-glacial tundra (Gramineae and *Artemisia*) has been found by Deevey (1951) in Aroostook County, Maine. This does not mean that a late-glacial flora was characteristic all along the ice border, but the discovery of such horizons, even if they exist, are subject to chance. Also, lacustrine pollen studies have not been made in critical regions such as Arkansas, Missouri, and Oklahoma. This new discovery for North America corresponds to similar evidence gathered by Degerboel and Iversen (1945) on the presence of late-glacial (Late Dryas) dry-steppe vegetation (Gramineae, *Centaurea Cyanus*, *Helianthemum oelandicum*, *Artemisia campestris*, and *Hippophae*) in Denmark. With the refinement of pollen analysis in America (surer identification, surer separation of pollen curves, more sensitive intervals), the late-glacial period may become more clearly defined.

The northeastward migration of the southwestern element was related to the presence and continuity of suitable habitats which were probably not only more wide-spread than today, but were also continuous. The most rapid migration of the xerophytes occurred along the uplands, and those plants such as juniper, with efficient means for dispersal, were the pioneers. Subsequently, as climatic conditions became more mesic, the woodland encroached, but frequent fires were very effective in slowing or preventing this encroachment. In modern times, as fires have become less a factor, the woodland has blanketed even the uplands, with the exception of the glades and knobs which are edaphic barriers to forest succession, leaving old open-growth Chestnut Oaks well hidden within the dense forests. Yet, fundamentally, the southwestern element of the flora is distinct and separate from the eastern and southeastern as pointed out by Adams, 1905. The most significant consequence of the northeastern migration of southwestern elements was the bringing together of species which had apparently been isolated from one another for a long time. The results might well have been a "freshening" of the germ-plasm of those species.

POPULATION STRUCTURE

Populations of junipers were sampled wherever the individuals were so numerous that random mass collecting was possible. In almost every population collected, the individuals were closely spaced in the cedar-woodland or cedar-brake type of stand. Isolated individuals were examined but not scored. Scattered individuals in oak-hickory woodland were studied but not scored as population pictograms. The distance between individuals in a population varies from widely spaced to so close that the branches touch all around. The amount of bare ground or thin cover determines their potential density in a stand.

Generally, junipers are found in areas which are in some early stage of succession or where a marked disturbance of the environment has occurred. The structure or pattern of any particular population depends on a number of factors, some inherent and others circumstantial. Junipers are classed as shade-intolerant plants. They grow best on well-drained, neutral, or alkaline soils. They have both deep roots and surface roots which enable them to compete successfully with bunch-grasses but not with sod-grasses. Therefore, these plants make the best growth as individuals and make the densest populations in dry, rocky soils with sparse cover or with clumps of vegetation surrounded by bare ground. Certain circumstantial factors affect the pattern of the population. Birds, especially the Thrush group, are the principal agents of dispersal of juniper seeds, but mammals, water, and gravity may play an important part. Populations spread, where topography allows, through the establishment of seedlings from seeds deposited by surface run-off water. The role of mammals, rabbits in particular, as disseminators of juniper seeds has been considerably underestimated. Wolf (1947) has made detailed studies of dispersal in two species and found that in open treeless country, rabbits are more important dispersal agents than birds.

If one assumes that in pre-human times fires were infrequent and the landscape was generally less disturbed than in modern times, the juniper was very likely confined, because of the pressure of competition, to the natural bad-lands such as cliff-edges and steep, rocky slopes. With the repeated burning-off of land in recent time, only those junipers remained which were in locations inaccessible to fire. In the last fifty years, fires have been substantially reduced and new areas have become available for invasion by the juniper. The source plants for recent migrations were those occupying cliff-edges and cliff-walls or in protected places. The present distribution of the most ancient specimens seems to bear this out.

COMPARATIVE MORPHOLOGY OF *Juniperus Ashei* AND *J. virginiana*

The differences between *Juniperus Ashei* and *Juniperus virginiana* are so great that one is almost unprepared for the fact that the two species hybridize so readily. The following table outlines some of the more outstanding differences.

<i>Juniperus Ashei</i>	<i>Juniperus virginiana</i>
1. Trunk more or less branched near the base; aspect generally bush-like; height to 35 ft.	1. Trunk single, erect; aspect generally pyramidal; height to 80 ft.
2. Foliage dense.	2. Foliage more or less open or plume-like.
3. Foliage yellow-green.	3. Foliage bluish-green.
4. Glands on leaves uniformly round, raised well above the leaf in a hemisphere.	4. Glands much elongated on certain leaf types, elliptic on others, seldom raised above the leaf.
5. Fruit large (6-8 mm. in diam.), with slightly resinous juicy pulp.	5. Fruit small (3.5-5 mm. in diam.), with strongly resinous dry pulp.
6. Seed 4-5 mm. in diam.; 1, rarely 2, per berry-cone, sharply pointed tip, no pits, smooth white hilum conspicuous, covering the seed at least one-third its length from the base.	6. Seed 2-3 mm. in diam.; 1 or 2 per berry-cone, rarely 3-6, blunt tip, numerous pits, small inconspicuous hilum.

Several of these differences merit further discussion.

1. BRANCHING PATTERN:

In general, investigators have considered a plant as either branching or unbranching and have let it go at that. When studied carefully, however, the branching pattern in *Juniperus* proves to be a character of value in separating not only species from species but also inter-specific hybrids from the parent species. In this study the central stem will be referred to as the primary shoot (axis); the main branches from the axis, whether in excurrent branching forms or multi-stemmed forms, will be called the secondary shoots (second degree of branching); the lateral branches from the secondary shoots will be called the tertiary shoots (third degree of branching) (fig. 1). The branching pattern in most junipers, especially of the SABINA section, is terminated by branching of the seventh degree (fig. 2). The more mesic species, *Juniperus virginiana*, may have branching to the fifth or sixth degree (fig. 2).

In *Juniperus* the vegetative portions of the plant are differentiated into short shoots ("spurs") and long shoots ("whips"). This difference is not as noticeable as it is in *Ginkgo* or *Pinus*, but the extremes of any one individual are quite as different from each other. In each species of *Juniperus*, leaf shape on the spurs differs from that on the whips. This has not been clearly indicated in most morphological treatments of the genus. In fact, adult whip foliage has been widely confused with juvenile foliage. The terminal portions, the long shoots or "whips", of the secondary shoots which are usually sheathed by a particular kind of elongated leaf, are called "terminal whips." The lateral branches of the secondary shoots, the tertiary shoots, may also be terminated by leaves of this elongated type, and these tertiary-shoot terminals will be referred to as the "lateral whips." Not all secondary shoots have terminal whips; for example, very old ones and those which have lost the terminals by accident or as the result of insect damage (twig borer).

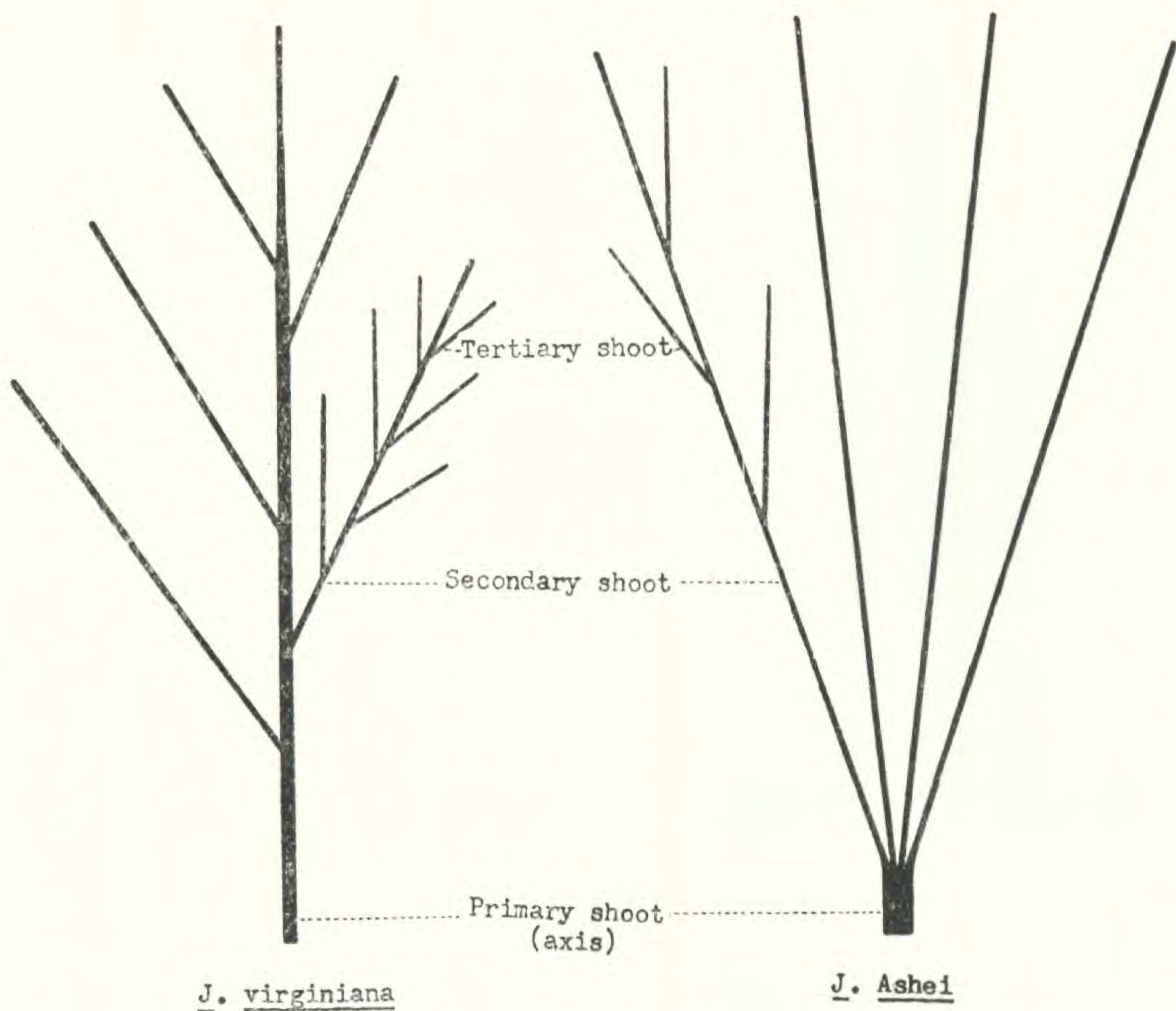


Fig. 1. Diagram of branching pattern.

Degree of branching was studied to determine whether there was any difference in this character between the two species. *Juniperus Ashei* was found to have a slightly greater degree of branching than *J. virginiana* (fig. 2). However, the tertiary shoots and their laterals are generally much shorter in *Juniperus Ashei* than in *J. virginiana*. The short branches of *Juniperus Ashei* give a dense, almost solid appearance and the long branches of *J. virginiana* a plume-like aspect.

Straight-trunked specimens of *Juniperus Ashei* are found only when the individuals are crowded so severely that defoliation of the lower branches results. Also, specimens are sometimes found with branches apparently diverging from a point at the ground level. Plants which in their early seedling stages have been grazed by goats or other animals have a bushy much-branched habit. Wolff (1948) reports that seedlings of *Juniperus Ashei* which have been cropped by goats make a growth resembling that of *J. Pinchoti*, the Redberry Juniper. He states that in such areas the two are so much alike in habit that other characters must be used to distinguish them. Usually, branches come out from a moderately buttressed axis close to but slightly above the ground level. These branches diverge and arc upwards in such a way that the plant looks like a giant tumbleweed. The tertiaries usually leave the secondaries or major branches at a wide angle, often at 90° . They apparently grow outward half their total length or less and then arc upward,

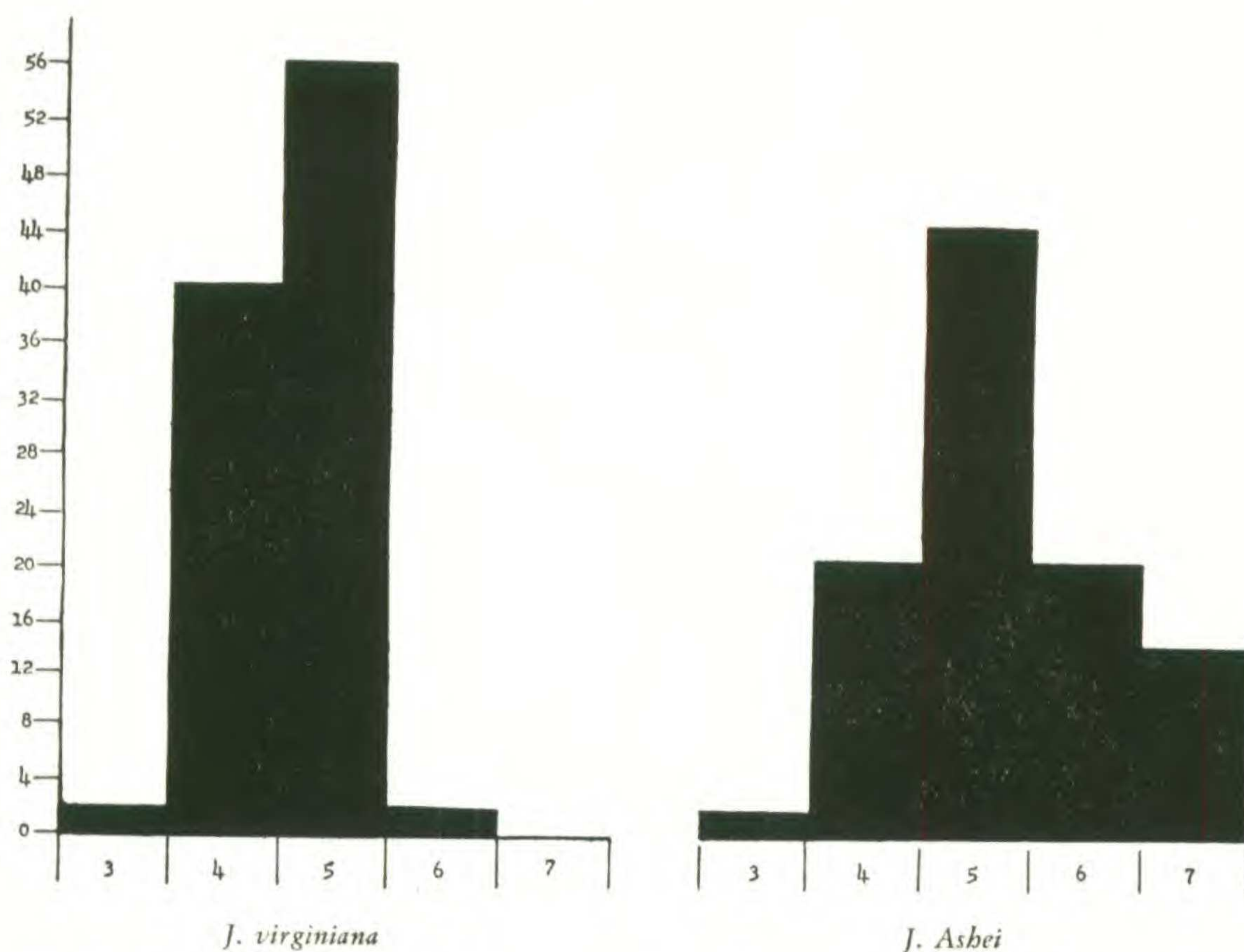


Fig. 2. Degree of branching based on counts from 100 tertiary branches of *J. virginiana* and of 100 branches of *J. Ashei*. Ordinate values represent frequency; abscissae, degree of branching from the major axis or axes.

further contributing to the dense bush-like aspect. The bark is often covered with a white patchwork of rings and splotches caused by a fungus, *Cyanospora albicedrae*. It is least prominent on plants of the bald knobs and White River bluffs of southwestern Missouri, and its occurrence on *Juniperus virginiana* is almost negligible. Some of the most bushy plants with very thick blunt branches but having technical characters more like eastern Red Cedar have been found heavily infected with *Cyanospora*. The most dense splotching occurs on the branches of pure *Juniperus Ashei* of the Edwards Plateau in central Texas. An Ashe Juniper infected with cedar-apple rust has never been reported.

The southwestern species may get to be 35 feet in height. On the Edwards Plateau most of the large old Ashe Junipers have long since been chopped and used for sills, railway ties, or posts. Approximately 4,000,000 acres of the Plateau adjacent to the Balcones Escarpment are now covered with cedars in various stages of maturity. A 4-inch basal trunk with 3½ inches of heartwood may be 50 years old. This corresponds to a 6-inch trunk at 50 years in *Juniperus virginiana* in Virginia. Likewise, if secondary shoots are cut the same distance back from the tip in *Juniperus Ashei* and *J. virginiana*, those of the former will be found to contain at least one and usually two more annual rings than those of the latter. Both species grow fairly rapidly, with eastern Red Cedar taking the lead.

Seedlings of *Juniperus Ashei* two feet tall may have from 7 to 9 well-developed, often eccentric, annual rings. Most of these seedlings have as much adult foliage as juvenile. The condition in Red Cedar is quite different. In Kentucky and Virginia, 2-foot seedlings have 4 or fewer annual rings and only juvenile foliage. On the Tennessee glades of the Nashville Basin ring transitions occur in slightly smaller-sized plants than characteristic of the "forest" tree type. However, on the bluffs and glades in the Ozark region and southwestward, 2-foot seedlings have 6-8 annual rings, and occasionally a specimen is found with slightly eccentric rings. In the same areas, where conditions are favorable, the seedlings develop in the fashion characteristic of the eastern forms. Now these phenomena can be readily explained as habitat responses; even the plants with eccentric rings may be suffering from severe root retardation on the short-radical side, which might correspond with the bluff side. But on the glades, many of which are relatively uniform habitats, these differences exist together. In hybrid swarms they are most obvious.

Juniperus virginiana in its typical form is a forest tree of stately proportions. In mesic habitats, such as the Interior Low Plateaus of Tennessee and Kentucky, it may reach a height of 80 feet or more and basal diameters up to 2½ feet. The aspect of eastern Red Cedar is indeed striking when compared with the shrubby or bush-like habit of most species in the genus. The lower branches on mature specimens growing in the open are quite long and usually arc downward about two-thirds their length and then upward to the tip. The bulk of the photosynthetic surface is then oriented in a plane tangent to the radial circle, which in effect makes the whole branch somewhat bilateral and contributes to the symmetry of the uniformly columnar crown and at the same time produces a maximum of green crown surface.

From the evidence based on clones of horticultural material, habitat does not seem to have a very great direct effect on habit, but in natural populations there are certain growth forms which seem to have been selected for particular habitats. In the Interior Low Plateaus of eastern United States there are two distinct habitat forms. One is the tall columnar tree found in open woods on relatively sandy or rocky limestone soils which do not support dense deciduous forest stands, or else on land which is kept cleared of forest by one means or another employed by man. Then there is the eastern glade or "barrens" form which is much less majestic, rarely being over 40 feet tall with secondary branches coming close to the ground. Of the glade plants, the lower branches are much longer in relation to the height of the tree, giving a more striking pyramidiform aspect. There are also recurrent types within these well-defined biotypes. The weeping form is commonly found in the lowest, wettest habitats, along creeks, rivers, or at the edges of swampy places. Sometimes, it occurs apparently at random in a population where no habitat factors seem to be involved. This weeping form is common to the genus as a whole and examples may be found in many species.

Symmetry of growth is of considerable importance as an aid to the study of introgression. The repeated branching system which is a prominent characteristic of the Cupressaceae and of *Juniperus* in particular is an interesting study by itself. One can determine by looking at the habit of each species what form the secondary and even the tertiary branches will display. In general, the branching system is repeated from the primary axis to the secondaries and the tertiaries. To prove that this is so does not require elaborate measurements. Several colleagues were invited to try grouping these secondary branches from each of five individuals into the five categories representing material from the individual plants. I had selected secondary branches from around the tree at a particular level and labeled them with an inconspicuous coding. After these branches were mixed, the sorting began. In every case these specimens were re-arranged into their original groups. The best method used was simply to hold the specimens in silhouette to the sky and compare their basic branching patterns. In *Juniperus* the exactness with which the replication of branching occurs throughout the plant depends on the relative purity of the species, for in areas where the species were thought to be relatively pure the replication was good, while in areas where hybrid swarms existed it was less exact. I was able to use branching system as a quick reference or clue to the relative degree of variability in a population.

Another method of demonstrating the replication of branching throughout the tree is to make drawings to the same scale of a number of branches of different order or degree and compare them with the same scale-drawing of the whole tree. This is laborious, but it gives measurable evidence of the importance of the branching pattern in variation studies in and between higher plant species. Such drawings were made of plants from near Glasgow and Bowling Green, Ky. (typical *Juniperus virginiana*); Grenada, Miss. (typical *J. virginiana*); Lesterville, Mo., and Gray Summit, Mo. (the Ozark type *J. virginiana*); Eagle Rock and Cedar Valley, Mo. (hybrid swarms); Busch, Ark. (hybrid swarm); Platt National Park, Okla. (hybrid swarm); Arbuckle Mountains, Okla. (typical *J. Ashei*); Kerrville, Tex. (typical *J. Ashei*); and New Braunfels, Tex. (hybrid swarm). The tree-to-tree and intra-individual variations in branching patterns showed the following trends: (1) least in populations of the two species away from the range of distribution common to both; (2) greatest in populations known to be hybrid swarms; (3) intermediate in areas suspected of having the influence of *Juniperus Ashei* even though no native specimens were in those areas. The area to which item (3) above applies is the central and northeastern portions of the Ozark Plateau. The tabulation and grouping of this initial data were preliminary to the population studies set forth in this paper.

With branching pattern data, one may distinguish between *Juniperus Ashei* and *J. virginiana* with 100 per cent accuracy, between individuals within either species with accuracy of about 90 per cent. Because of such symmetry, there are a great many similar branches at various levels on the tree which enables one to sample material reasonably free from environmental variables.

In most good species of higher plants, those with discontinuous differences and with simpler variation patterns than those of a species complex, this relatively accurate replication of branching within individuals may be a fundamental character for contrasting each against the other. It is the presence of disharmonic variation (the lack of accurate replication from branch to branch) which gives the first clue that a particular individual may be a hybrid. Interspecific hybrids in *Juniperus* are more variable within themselves than are pure individuals. This disharmonic variation is probably the result of the conjoining of two different systems of growth. Such ideas have been elaborated upon by D'Arcy Thompson (1942) and Huxley (1932). The less extensive or more subtle the introgression the less obvious is the morphological or physiological expression. This clearly indicates the inter-dependence in science of data from various sources. If it had not been for the years of work in groups of organisms which could be tested with expedience (Heiser, 1949), it would be nearly impossible to understand what has happened in *Juniperus*. Even hybrid swarms among the species are difficult to study, but they offer rich material as to what happens when germ-plasms are mixed up. In *Juniperus* the most obvious situation is in the hybrid swarms of *J. pachyphloea* and *J. scopulorum* in east-central Arizona and west-central New Mexico, where a juniper which resembles live-oak in bark and branching characters, with fruit as large as a pecan, is hybridizing with another juniper which looks quite like eastern Red Cedar. The most obscure picture is that of the hybrid swarms of *Juniperus scopulorum* and *J. virginiana* in the middle-western United States. Here the Red Cedar and Rocky Mountain Juniper are so similar as to require practically a statistical study of their characters to separate them.

2. FOLIAGE DENSITY:

Foliage density is a very good character to delimit the species in the field and even offers aid in spotting recombinations. Although such a character is not free from environmental modification, direct or indirect, when density is contrasted with other characters on the same specimen, some information comes to light which is not to be found in most examples of progressive adaptation to xeric conditions. For occasional individuals in populations known to be hybrid swarms, on McVey Knob, Branson knobs, and Platt National Park, the density may vary on a single plant all the way between that characteristic of each species. This tendency also holds for other characters. The difference in density is primarily due to the number of laterals per unit length of the secondaries or tertiaries, and this is again related to the comparative growth rates of the two species. Thus, in *Juniperus Ashei* there are many more lateral branches per unit length of the secondaries and tertiaries, and these typically are considerably shorter than in *J. virginiana*. When length of laterals is plotted against number of laterals, the values for *J. Ashei* do not overlap those for *J. virginiana* until values for the populations on the Ozark glades are interjected.

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Three selected populations were studied in detail in relation to foliage density, an open field and a glade population of *J. virginiana* at the Missouri Botanical Garden Arboretum at Gray Summit, near St. Louis, Missouri, and a population of *J. Ashei* on the Edwards Plateau near Kerrville, Texas. At the Arboretum the open field and glade population are only two miles apart; yet the foliage density in the open field group is like that in eastern Red Cedar while that of the glade group is clearly intermediate between the eastern and the southwestern species. The habitats are not the same by any means. The main thing they have in common is that each is largely covered by grasses and junipers.

3. FOLIAGE COLOR:

The color forms in *Juniperus virginiana* are too numerous to treat here. For purposes of contrast a few generalizations will suffice. Typical eastern Red Cedar is dark green, frequently with a slight bluish tint. One common color form found throughout the range of species is the bluish-glaucous one. Yellow tints are rare in *Juniperus virginiana*.

Juniperus Ashei is a deep olive green with a conspicuous yellow cast except in hybrid swarms. In hybrid swarms there are found some plants (taxonomically *J. Ashei*) with blue-glaucous foliage and some with very dark green almost black foliage growing side by side with plants having the typical *Ashei* color form seen in the Arbuckle Mountains or the Edwards Plateau. These color recombinations are especially noteworthy in the bald-knob country of southwestern Missouri (Bald Knob southwest of Hollister on Highway 86).

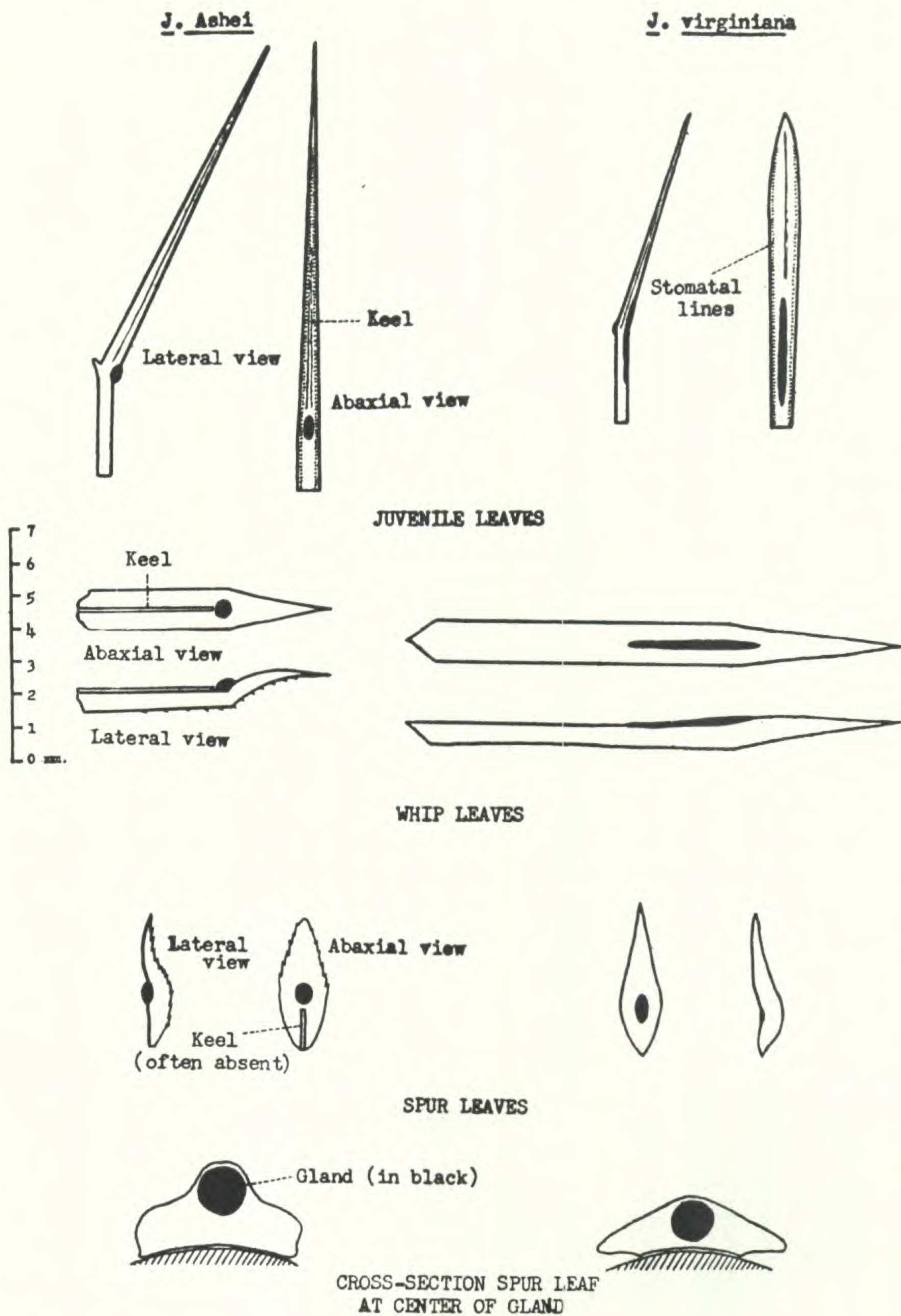
The color of the portions of those shoots which are just becoming woody is a fairly dependable character for contrasting the two species. Young woody twigs of eastern Red Cedar are typically dark brown, usually tinged with gray but sometimes with red. The young twigs of Ashe Juniper are a bright conspicuous rust-brown. As they age they become gray until finally they have an ash-gray hue.

Because of the highly subjective nature of color judgment, even with the aid of complete color charts frequently used in animal taxonomic work, color characters were not utilized in the pictorial population graphs.

4. GLANDS:

The glands are good characters for contrasting the two species, both the whip-leaf glands and spur-leaf glands being quite different in their typical form.

Whip-leaf glands.—In Red Cedar these are typically much longer than wide. On vigorous whip shoots the leaves are 10–14 mm. in length. The ratio of gland length to gland width ranges from 6 to 12. In typical *Juniperus Ashei* these leaves are from 4 to 7 mm. in length, rarely 8 mm., while the ratio of gland length to width is usually 1, sometimes 2 (fig. 3). This means that in the eastern species a leaf 12 mm. long may have a relatively flat, elongate-elliptic or tear-drop gland on the back side 6 mm. in length and 0.6 mm. in width, a ratio of 10. Usually, this gland extends toward the tip of the leaf past the juncture of the sheath and

Fig. 3. Leaf morphology of *Juniperus Ashei* and *J. virginiana*.

the blade. In the southwestern species a leaf 7 mm. long may have an almost perfectly round raised gland from 0.5 to 1 mm. in diameter. The gland gives the appearance of a small BB shot placed on the back of the leaf at the juncture of the sheath and the blade.

In hybrid swarms the gland measurements vary between the values for the two species along with many unusual combinations of the other characters. In the areas where influence of *Juniperus Ashei* is suspected in *J. virginiana*, the gland measurements are intermediate.

Spur-leaf glands.—In Red Cedar these are typically elliptic, flush with the lower surface of the leaf, and rarely exceeding 1 mm. in length. They are invariably farther than their own length back from the leaf tip. In Ashe Juniper the spur leaves may be glandular or eglandular. If glandular, the glands are usually slightly less than 0.5 mm. in diameter and are situated at the juncture of the sheath and the blade. They are also slightly raised above the abaxial surface of the leaf but not so much so as on the whip leaves. Well within the range of the species these leaf glands vary but little, but at the commissures of distribution of the two entities many interesting variations occur, sometimes within a single plant. In hybrid swarms, specimens of *Juniperus Ashei* are found without eglandular leaves but with typical glands on some spurs and elliptic raised ones on others. Leaves of *J. virginiana* in such a location are never eglandular, but the glands are even more variable though often very small and inconspicuous. In some of the *virginiana*-like hybrids, glands may be found here and there which, if considered alone, would identify the specimen as *Juniperus Ashei*.

5. FRUIT:

Most Junipers are dioecious. However, both megasporangiate and microsporangiate strobili are often found on the same plant, but one or the other type is always in much greater abundance. The seemingly simple fruit of *Juniperus* is such a morphologically complex structure that an analysis of its variation must be preceded by a technical discussion.

In the SABINA section the megasporangiate cone is generally formed from six scales. The cone appears in the fall, borne terminally on dwarf or short axillary shoots from branches of the current season. The sporophylls become recognizable only a few weeks before pollination, when at least two pairs of them grow up over the ovules and coalesce to form the berry-cone. The berry-cone consists of two or more pairs of opposing sporophylls. The fertile sporophyll-pairs are central on the cone axis with sterile sporophyll-pairs above and below. Sometimes only one sporophyll of a pair is fertile. When the berry-cone approaches maturity, the "fruit-scales" appear on what is morphologically the upper side of the sporophylls and contribute the bulk of the fleshiness of the mature structure.

The young buds become visible just prior to pollination. As the fruit scale primordia grow, the sporophylls are pushed away from the ovules making them plainly visible in their "nest." Later the "fruit-scales" grow up over the ovules

and seal them within the "berry." In some species the sporophyll tips are quite plainly visible about the sides of the berry-cone, while in others they are almost imperceptible.

The fruit of both *Juniperus Ashei* and *J. virginiana* matures in one season. In both species flowering occurs annually, but the extent of the crop varies a great deal from plant to plant and from year to year. Usually, a heavy crop is produced every third year. The southwestern species bears much larger crops of fruit which frequently appear as dense "clusters", giving the aspect of bunches of grapes.

In *Juniperus Ashei* the young ovulate strobili appear from mid-winter to mid-spring and may be found fully ripened from September to December. There seem to be no critical factors affecting flowering time decisively. Both Ashe Juniper and Red Cedar begin to flower later in Missouri than in Texas. Because of the overlap in flowering time, plants of the two species, wherever they occur together, may utilize pollen of either or both. By mid-February the staminate cones have shed their pollen.

The ovulate cone consists of 3 ternate scales (a single whorl) or, more commonly, 2 pairs of decussate scales. The sporophyll tips or scales (those which become a tiny flap on the fruit coat) are finely toothed on the margin. The lower sporophyll pair usually has one fertile member resulting in a single-seeded berry-cone. Often the two upper bracts or leaves contribute to the fleshy mature "berry," but they invariably remain at the very base of the fruit. Just after pollination the sporophylls elongate rapidly, so that the young cone becomes about twice as long as wide and looks like a tiny urn. Then the fruit scales begin to grow and completely close over the ovules, pushing the sporophyll tips apart and increasing the girth of the fruit. Generally, the length of the mature berry-cone is 1 mm. more than its width, which may be from 6 to 8 mm. The sporophyll tips are very conspicuous in the fresh, mature berry-cones but with age may slough off or dry up.

In *Juniperus virginiana* the young ovulate strobili become evident toward the end of February just prior to pollination, which in the Ozarks generally occurs the first week of March. Ottley (1909) reported that seasonal variation in pollination time in *J. virginiana* amounted to as much as two weeks in Massachusetts. Spatial variation in the occurrence of stages of the reproductive cycle is quite marked. In general, there may be as much as a month's difference in time of flowering, pollination, fertilization, and final ripening, from Texas to New England.

The cone consists of two pairs of sporophylls, one or both of the lower pair being fertile, while the upper two are sterile. Sometimes a third pair develops, resulting in a cone with the fertile pair of sporophylls tipped by 2 pairs of sterile ones. The mature berry-cone often shows 6 tips or wrinkles on its fleshy periphery. This usually reflects the role of a pair of subtending bud scales in the construction of the cone. Ordinarily, there are 4 wrinkles or tips which are the remnants of the sporophyll tips after the growth of the fruit scales.

Mathews (1939) has described three types of flowers for *Juniperus virginiana*: (1) with one ovule in the axil of one member of the fertile sporophyll pair, (2) with two ovules side by side in the axil of one member of the sporophyll pair, (3) with one ovule in the axil of both members of the fertile sporophyll pair. He reported that about two-thirds of the flowers were of type 1, and the rest were divided equally between types 2 and 3. These observations seem to be best supported by the plants in southern and southwestern areas. The flower types were usually distributed in such a way as to be relatively constant for a particular tree. Either the types occur in the above proportions on a given tree, or type 1 predominates, or types 2 or 3. There was no clear geographical pattern of distribution for these flower types, but in the northern range the frequency of 2-seeded berry-cones is greatest.

When mature the berry-cones range in size from 3 to 5 mm. in diameter. This variation in size shows an interesting geographic distribution. In the range of Red Cedar, with the exception of the Ozark Plateau and southwestward, the mature berry-cones normally measure 4 mm. across. Rarely, cones 3 and 5 mm. across are found on a particular tree. In the Ozark Highland, in Oklahoma, and in Texas east of the Balcones Escarpment, the berry-cones vary in size, but those measuring 5 mm. are most typical, and the 4-mm. and 6-mm. sizes are found in about equal abundance. One would expect to find a species well adapted to mesic habitats to express a major size modification in all its characters, as its range expands into more xeric environments. This is not so for the berry-cones, since their average size actually increases towards the southwest. The key to the significance of the variation in size lies in the behavior of this character in hybrid swarms where sizes range from one species to the other. The most significant fact is that the various patterns of size and shape of berry-cones occur with varied combinations of other characters of the two species, resulting in an inharmonic and heterogeneous population explicable only in terms of hybridization.

6. SEEDS:

The seeds are good taxonomic characters in the genus, being mostly very different in the different species. They were not used in the scoring of populations, but they were often referred to simply as a check. In hybrid swarms especially, seeds were examined. In plants obviously intermediate in other characters, the seed varied between forms typical for each species.

The seed of *Juniperus Ashei* typically is 6 mm. long by 4 mm. wide and very sharply conical with an almost flat base. The base is covered with a conspicuous white hilum which may extend as much as one-third the length (2 mm.) up two opposite sides. The mature seed is invariably dark chocolate-brown except at the hilum. There may or may not be grooves along the sides formed by the pressure of resin canals as the ovules grow. Normally, there is one seed per fruit, occasionally two, the two-seeded condition being frequently accompanied by other interesting characters. Fruits with two seeds are most common in plants from

Ft. Worth to San Antonio, a region where hybrid swarms are common. Such seeds are not typical of *Juniperus Ashei* in color or hilum structure, since they are usually whitish to light yellow-brown and have very variable hilum shapes and sizes. Many seeds of one-seeded fruits found in this same region also vary considerably in color, size, shape, and pitting. Significantly, the variation is in the direction of *Juniperus virginiana*. The most common type of seed in a hybrid colony is one intermediate in size and in shape, with a few small bumps on the surface, and of a basic yellow-brown color thoroughly speckled with chocolate-brown everywhere except on the hilum. In such cases the hilum is usually very variable in size and shape (pl. 1).

In *Juniperus virginiana* the seeds are very small, usually 2 to 4 mm. long by $1\frac{1}{2}$ to 3 mm. wide near the base. They are bluntly pointed and typically a very light slightly yellowish-brown. In the Ozark region the seeds are not only more frequently single, but also slightly darker, and show some variation in hilum size and shape. On the glades these characters are quite as variable as any of the others. In the hybrid swarms of southwestern Missouri the seeds are as have been described for similar situations along the Balcones Escarpment (Ft. Worth south to San Antonio).

Exserted seeds are quite common on specimens of *Juniperus Ashei*. Such seeds are much larger and more elongate than typical seeds; and from one-third to one-half their length is exposed at the apex of the fleshy berries. In every exserted seed examined insect detritus was found. In an infected tree the fruits are usually characterized by exserted seeds (a much rarer phenomenon in *Juniperus virginiana*). This condition is common in *Juniperus*. Every species which I have seen in the field has shown it to some degree. Martinez (1946) has reported this teratological condition in species of *Juniperus* in Mexico.

7. TERMINAL WHIP:

The amount of long shoot growth on the secondaries (main branches) of mature plants is very different between specimens of *Juniperus Ashei* and *J. virginiana* of the same age. Plants must be at least mature before this character becomes useful in interspecific diagnoses. Youthful individuals of all species tend to have a great amount of long shoot growth per season. The long shoots were measured from the tip of the secondary back to the point where the shoot becomes woody. This is a somewhat arbitrary unit since the age of that position of the long shoot is slightly different for each species. However, this makes the character doubly good for our purposes, since it measures two differences at once. Two and sometimes three sub-regions of the terminal whip can be distinguished by the color and texture of the whip leaves. The region nearest the apex is, of course, the current season's fresh foliage. This is bright green and soft-succulent. Next is a length of yellowish tough foliage followed by one of brown woody foliage on which the whip leaves are still completely distinct. This constitutes all of the terminal whip; beyond this point the twig is grayish, woody, and sheathed with whip leaves whose bases are ruptured and in various stages of sloughing off.

In *Juniperus Ashei* the terminal whip is produced at a slower rate so that there is less whip length per year as judged by annual rings. The terminal whip always runs into the third year's growth. It is heavier, denser, and more rigid than that in Red Cedar. The leaves are ternate on these shoots except on some specimens in hybrid swarms.

Mature specimens of Red Cedar have much longer terminal whips than *Juniperus Ashei*, except in certain areas of the Ozark Plateau and in hybrid swarms. This whip runs into the second year (as judged by annual rings) but not the third year. Third year growth is well into the woody portion of the stem. The whip may have ternate leaves or decussate ones. The percentage of ternate foliage on the whips increases towards the southwest.

8. LATERAL WHIP:

The amount of long shoot growth on the tertiaries (lateral branches to the main ones) is quite different in typical plants of the two species. This character may only be used to contrast mature plants of nearly the same age. It is a variable character at best, but in young specimens it is too variable to be of any value. This character was utilized in the same way as the terminal whip. The lateral long shoot growth bearing distinct non-woody whip leaves was measured.

9. LEAVES:

There are three types of leaves common to most species of *Juniperus*, the SABINA section in particular. These are the acicular leaves characteristic of the *juvenile* foliage of seedlings, the elongate *whip* or long shoot leaves characteristic of the terminal and lateral extremities of the secondary and tertiary axes, and the small usually overlapping scale leaves whose bases are closely appressed to the *spur* or short shoot axes (see fig. 3).

Juvenile Leaves.—Both species are dicotyledonous. The seed-leaves are followed by acicular leaves which are the sole leaf type for three to five years or more, depending on the environment. Seedlings growing in a well-drained soil with no shading may develop adult foliage within three years. Those seedlings growing beneath other trees where shade is intense may not develop adult foliage for several years, and even then they will often retain some juvenile foliage indefinitely. Frequently in trees which suffer localized root injury, juvenile foliage is subsequently developed on portions of the plant, usually on the side of the injury. Such traumatic response is evidenced in new growth following a rock slide which does obvious injury to portions of the root system. Juvenile leaves vary in size rather markedly with different environmental conditions. In general, when juvenile foliage develops on a mature plant, its elements are proportionately smaller than those on seedlings.

In seedlings of *Juniperus Ashei* the juvenile leaves are normally 3-ranked, sometimes 4-ranked or rarely 5-ranked. A *typical* leaf has a sheathing base 2 mm. in length and fused with the axis, while the blade extends out from the axis at a nearly right angle to a length of 10–15 mm. The sheath and the widest part

of the blade, its base, are 1 mm. wide. The raised or humped gland is 1 mm. long and 0.3–0.5 mm. wide and is inserted half on the sheath and half on the blade. There are narrow stomatal lines on both surfaces on each side of the mid-vein. The mid-vein is conspicuous on the abaxial side and inconspicuous on the adaxial.

In *Juniperus virginiana* these leaves may be decussate but are usually 3-ranked, rarely 4-ranked. The sheath is 2–5 mm. long, and the blade is 8–12 mm. long. These leaves are 1 mm. wide along the sheath to a point on the blade nearly half-way to the leaf tip.

Whip Leaves.—These elongate leaves are even more different between the species than are the juvenile leaves. They are also quite different from juvenile ones. The differences are numerous but the most conspicuous one is in the ratio of sheath to blade. In juvenile leaves the blade is more than twice longer than the sheath, while in whip leaves the sheaths are longer than the blades.

In *Juniperus Ashei* a typical whip leaf is 1 mm. wide and has a sheath and a blade 4 mm. and 3 mm. in length, respectively. The abaxial gland is approximately 0.4–0.8 mm. in diameter and is a hollow sphere filled with a thin clear resinous liquid, seemingly a turpine complex. It is situated at the juncture of the sheath and the blade. The sheath usually has a thin keel extending to the base of the gland. The sheath and the blade of these leaves have teeth along the margins which are barely visible when magnified 12 times, but show up plainly at magnifications of 20–40 times. At higher magnifications these teeth are seen to be the result of occasional “spurs” or bends in certain of the epidermal cells of the margin. These large marginal cells are lined up at an angle with the longitudinal axis of the leaf.

In *Juniperus virginiana* a typical whip leaf is 1 mm. wide with a sheath and blade 9 mm. and 4–5 mm., respectively. The abaxial gland is a long hollow cylinder 2 to 5 mm. long and from 0.25 to 0.4 mm. in cross-section. However, on the back surface of the leaf this gland shows only as a thin line less than 0.2 mm. in width, no more than the width of a fine pencil mark. Most of the gland is on the sheath, but it extends along the blade a small portion of its length. The sheath is not keeled. The underneath surface of the blade has two longitudinal, fairly wide stomatal lines on each side of the very blunt mid-vein. The margins of the sheath and blade are smooth or very slightly undulate, never toothed. The marginal epidermal cells have their long axes nearly parallel to the longitudinal axis of the leaf and fit together smoothly with no out-jutting “spurs.” The leaves are often covered with a white bloom which obscures the thin abaxial gland.

Spur Leaves.—These vary in size depending on their position in relation to the growing point from which they originated. In *Juniperus Ashei* a typical spur leaf has a sheath $1\frac{1}{2}$ mm. long and a blade the same length. Where glands are present, they are round and raised and situated about $\frac{1}{3}$ the distance from the base of the leaf. The sheaths are often keeled, and the blades are usually markedly humped. In *Juniperus virginiana* a typical leaf sheath is only 1 mm. long, while the blade

is 3 mm. long. The gland is elliptic and flat against the surface or slightly sunken and in the same position as described for *J. Ashei*.

In hybrid swarms many variations between the two leaf types occur. A plant may be found with every character of *Juniperus Ashei* except that it has a straight columnar habit and *no teeth* on the leaf margins. Specimens may have an intermediate leaf type, or both types together, or various intergradations of the two.

10. MICROSPORANGIATE STROBILI:

The pollen-bearing cone in *Juniperus* generally consists of four rows of shield-shaped sporophylls. The sterile part of the shield adjacent to the young sporangia grows downward and forms the mature peltate sporophyll. The sporangia are marginal and appear on the abaxial side at the base of the sporophyll.

In *Juniperus Ashei* the cone is made up of 12–18, usually 14, microsporophylls which have broadly rounded, abruptly acuminate, nearly mucronate tips and, like the leaves, have teeth on the margins. There is a small round flat gland approximately centered on the abaxial side. In Texas these cones may become visible late in December and usually have opened and shed their pollen by the middle of February.

In *Juniperus virginiana* the cone consists of 10–12, rarely 14, entire-margined sporophylls usually with blunt round apices. A conspicuous, somewhat elliptic gland is centered on the abaxial side of the sporophyll. These cones become recognizable as such in the Ozark region toward the last week of July and by early September contain mature microspores. Mathews (1939) reported that in North Carolina they are visible in August and pass the winter filled with microspores. According to Ottley (1909), in Massachusetts the cone develops much later and overwinters with microsporangia containing microspore-mother cells.

Where the ranges of the two species overlap, the whole cycle of reproduction also overlaps, so that the degree of open pollination which will be interspecific depends on local conditions for each individual. If conditions for pollination by either species are equally good, then Ashe Juniper pollen will dominate in the population. Ashe Juniper produces enormous quantities of pollen, while Red Cedar produces comparatively little. This fact is no doubt largely responsible for the difference in the extent of influence of the two species upon one another. Where there are large populations of both species in the same area, the bulk of the specimens of *Juniperus Ashei* show little effect of mixing while the specimens of *Juniperus virginiana* show a great deal. This fact complicates any attempt to draw conclusions as to adaptive or selective advantage in members of the hybrid swarms on the basis of the character combinations established there. In other words, there are a number of theoretically possible gene combinations which are not realized because of this tendency toward unidirectional flow of germ-plasm. This is not to say that the influence of *Juniperus virginiana* on *Juniperus Ashei* is ill-defined or slight in degree, far from it. Specimens of Ashe Juniper from along the Balcones Escarpment show quite extreme combinations of characters of the eastern species, as much so as in the other direction. However, the actual amount

or mass of the effect is much less to the southwestern species, since it so well outranks Red Cedar as a pollen producer.

In hybrid swarms there occur combinations of microsporophyll characters. The most evident trend is that specimens of *Juniperus virginiana* tend to have much more irregular-margined, occasionally some erose-margined sporophylls. There is also much variation in sporophyll shape, especially in relation to the apex characters.

11. WOOD:

The heartwood of *Juniperus virginiana* is bright pink-red when fresh and fades to a dull brown-red. The pigment is reported to be very similar to that of *Sequoia*. Eccentric rings are very rare. In *Juniperus Ashei* the heartwood is a light dull brown. Eccentric rings are common. The heartwood to sapwood ratio is slightly greater in this species.

In eastern United States freshly cut cedar is completely homogeneous in heartwood color; in the Ozarks it is not. Brown heartwood increases in abundance as one approaches the Southwest. Often in Red Cedar trees from Ozark river bluffs and in multi-stemmed individuals, a dull brown heartwood is found, although in others it is a pink-red.

STUDY OF VARIATION

It was necessary to find dependable characters which would indicate as accurately as possible the degree of hybridization between the two species. This required a survey of the variation within each species in areas where contamination was least likely. Characters were then chosen with regard to their degree of independence, variability, and difference. These were to be contrasted in population studies over as much as possible of the total ranges of both species.

The method of determination of suitable characters was inevitably laborious. Ideally, complete genetic analyses of the behavior of characters are needed in order that character correlations may be carried on with complete confidence. On superficial examination, it often appears that multiple-character correlations make something difficult and messy out of something easy. Good unit characters are seldom characteristic of species. Many apparently good species are differentiated only by contrasting several (usually quantitative) characters. Since multiple-factor characters are the basic genetic material in population dynamics, it seems necessary to employ multiple correlations in order to demonstrate the nature of differentiation within the population. The analysis of the behavior of a single character in a population can only lead to conclusions concerning that single character. The presence of a cline of variation which demonstrates intermediacy is not evidence that the intermediates are the result of hybridization. Hybridization can be inferred only from variation patterns which demonstrate recombinations of characters. Combinations of characters are the clues which rule out other conditions causing intermediacy—environmental modifications, differential selection of intraspecific gene patterns, divergence preceding isolation.

The first problem, environmental modification, may be solved by experiment or perhaps by careful observation in the field. The second, differential selection, is not so easy when only a single character is employed. Intermediate environments may select intermediate characters, but differentially; that is, some characters may be selected more strongly than others; thus a single character study is not so reliable in demonstrating the cause or causes of variation. The marginal waifs and transition-zone variants show up markedly when multiple correlates are utilized. The third factor, divergence preceding isolation, involves timing. How can one tell, from single character clines, which end of the variation spectrum he is observing? Is he observing divergence consequent to isolation or allopatric hybridization? The multiple-correlation technique offers greater security in two ways: after one roughly determines the behavior of several characters under different environmental conditions, he may study their synthetic behavior, which demonstrates whether they have the structure of recombinations and how well they are linked, or whether they constitute continuous clinal gradients. The multiple correlation scheme is, in brief, a much better description of what the organisms of a population are doing.

The subtleties of correlation suggested above are not so serious in studies between two species well differentiated morphologically and ecologically. Interspecific variations are usually not so cryptic as intraspecific ones. I repeat, that if introgression is occurring in *Juniperus* it should give evidence in four ways: (1) that the species in question will hybridize. (This may be experimental verification or the presence of hybrid swarms where the species occur together); (2) that there are recombinations of the characters from the species in question; (3) that when characters of one species occur in the other they become progressively more "dilute" away from the region of hybrid swarms; and (4) that the characters which differentiate the two species should be at least slightly correlated throughout the area of introgression.

It is only in an analysis of the patterns of recombinations of more than one character, preferably of many characters, that introgression can be inferred. Even multiple correlations may not constitute proof of introgression but are the working basis for an hypothesis which may subsequently be tested by experiment. The experiments must meet two general requirements: (1). They must indicate through controlled breeding that the morphological and/or physiological patterns which arise by crossing species are similar to the situations found in nature. (2). They must show that these patterns cannot in like manner be produced by other factors—specifically, direct modification through environmental action.

In this study it has been possible to check only the second general requirement, since this work on *Juniperus* is inductive and deductive with only a small amount of strictly experimental evidence. The conclusions, therefore, are products of inference and in the rigid sense of scientific discipline may not be taken as proof.

Since morphological characters may vary a great deal in sensitivity to environmental effects and likewise in their genetic stability, it was desirable to select those which would be the most sensitive index to ecological differentiation and at the same time indicate possible ways in which their potential of variation was initiated. It would do little good to use characters for contrast which are so stable that under natural conditions only very slight variation occurs; in consideration of the antithetic situation, extremely morphoplastic characters are also objectionable. Most characters of *Juniperus* are intermediate in these respects, possibly with a slight edge toward morphoplasticity. Both types of characters were available and both were used for a special reason. Those which fluctuated somewhat were separated from the more stable ones by studying the morphology of hundreds of individuals throughout the range of the two species and by ascertaining the behavior of these characters in horticultural varieties throughout the range of *J. virginiana*. A character was considered fluctuating if it expressed a high degree of variability. Conversely, a character was considered stable if it remained constant throughout the range of the species. This particular part of the investigation was made only in those areas where the two species were far from contiguous.

If one could show evidence of recombinations of the fluctuating characters where the variance of the character in any particular individual was no greater or less than could be expected in either species in the same area, while the stable characters were varying within the individual much more than could be expected, then it could be inferred that this variation was the result of recombinations through hybridization.

Individuals in natural populations at the Missouri Botanical Garden Arboretum, Gray Summit, Missouri, were studied at first to determine what characters of *Juniperus* would be most suitable as an index to purity or hybridity. Later, these characters were extensively checked in areas known to have homogeneous (concordantly varying) *Juniperus virginiana*, and again in areas known to have typical *J. Ashei*. The following six characters were analyzed in detail as to the degree of variation from one branch to another on a single tree, their relative independence, variability, and significance as an index of difference:

1. Ratio of gland length to gland width.
2. Length of a typical terminal whip leaf.
3. Length of terminal whip at the apex of a typical secondary shoot.
4. Length of lateral whip on the same secondary shoot.
5. Per cent of decussate spur shoots on the secondary shoot.
6. Leaf margins, scored as smooth (S), denticulate (D), or intermediate (I).

The characters also had to be checked for their seasonal variability. Of the characters discussed under "Comparative Morphology," the six listed proved to be most convenient and dependable. The sex was recorded in order to check for any possible correlation with the other characters. In so far as possible the diameter of mature berry-cones was recorded. Seed characters were carefully studied for all populations and proved to be very stable. Unfortunately, seed characters were

far from convenient to use as a measure, but they were used as a parallel to the others as an indicator of hybridization.

MEASUREMENT OF CHARACTERS

The measurement of these six characters involved population sampling over a considerable area. For convenience, each sample compilation will be given a group number for each species.

Juniperus Ashei:

Group A-I.—A survey of the general area was made. More than 200 specimens were measured by traversing the Edwards Plateau of Texas (Comanche Series of the Cretaceous) from Junction to Garner State Park to Boerne and thence to the east of the Central Mineral Region and north to Stephenville.

Group A-II.—A survey was made of regions where *Juniperus Ashei* is found growing in the vicinity of *Juniperus virginiana*. This was along the base of the Balcones Escarpment (Gulf Series of the Cretaceous) from New Braunfels to

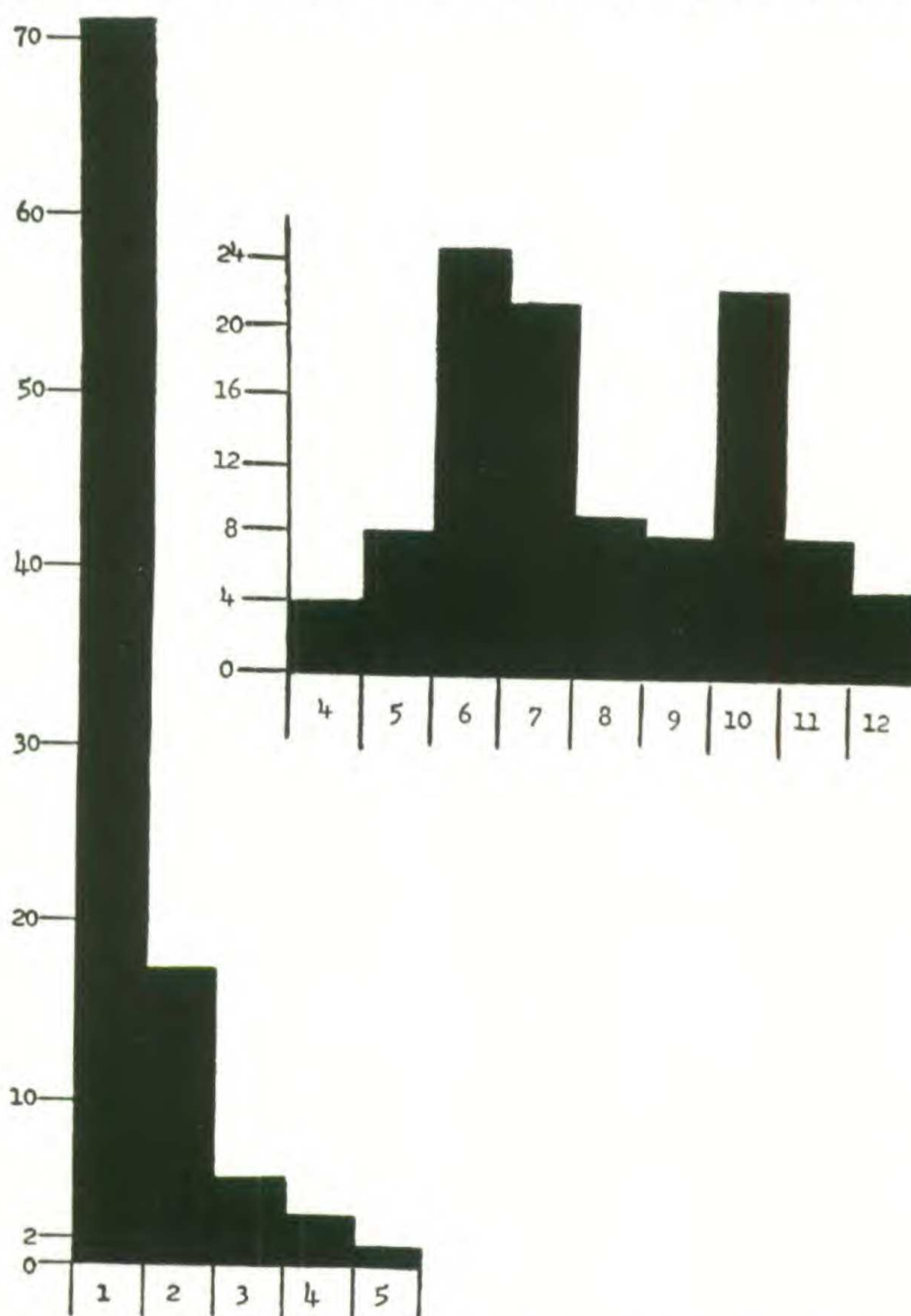


Fig. 4. Ratio of whip-leaf gland length to width from 100 specimens of *Juniperus Ashei* (left), and from 100 specimens of *J. virginiana* (right). Ordinate values represent frequency.

Austin to Georgetown to Waco. Twenty-five plants were measured in populations near the cities named.

Group A-III.—Twenty-five specimens in the Arbuckle Mountains, Murray County, Oklahoma, were measured.

Juniperus virginiana:

Group V.—A survey was made of the regions where this species grows as a tall forest tree removed from other species. One hundred plants were measured from populations of southern Indiana, Kentucky, and Virginia, respectively.

When the six characters in groups A and V were compared, each was repeatedly found to be useful as an index of morphological affinity; in other words, an individual juniper may be fairly exactly placed in terms of specific reference to these characters. Graphs for each character demonstrate the differences between the A and the V groups (see figs. 4-8).

1. RATIO OF GLAND LENGTH TO WIDTH:

This value had a constant value of 1 in Group A-I. In Groups A-II and III the ratio varied from 1 to 5: 80 per cent had a value of 1; 10 per cent, 2; 5 per cent, 3; 3 per cent, 4; and 2 per cent, 5. The frequency of the higher values increased northeastward.

In Group V the values for the ratio varied from 4 to 12. The total curve for 100 specimens was bimodal. The primary mode was 6 while the secondary mode was 10. The bimodality was contributed by values of a single population from Virginia, which were the highest of all measurements made except those for southern Michigan and Pt. Pelee, Ontario, where *Juniperus virginiana* grows in the same habitat as *J. horizontalis*, which also has a mode of 10 for this character. The median was 7 and the mean 6.9 (see fig. 4).

2. LENGTH OF TYPICAL TERMINAL WHIP LEAF:

Originally, this character was measured by taking the total length of all the terminal whip leaves and dividing by the number of them. Later it was found that the average length of three leaves equally spaced on the whip shoot was satisfactory.

In Groups A-I, II, and III the values ranged from 2 mm. to 14 mm. with the mode at 4 mm., the median at 5, and the mean at 5.5. Beyond the value 9 there were only 3 measurements of 10, 3 of 11, and 1 of 14. The values had a very definite geographical pattern of distribution, for the extreme measurements, or those more characteristic of *Juniperus virginiana*, were found only in regions where the two species occur in proximity. Values from 2-6 were in Group A-I; values from 7-14 were in Groups A-II, III. The range of values in Group V was from 4 to 16 mm., with the mode at 8 mm., the median at 9 mm., and the mean at 8.95 mm. From Virginia toward the Shawnee Hills there was a tendency toward slight reduction in leaf length. (See fig. 5 for a graphic representation of the whole.)

3. LENGTH OF TERMINAL WHIP:

This character was measured as described in the section on "Morphology," from the apex back to the point where the shoot is obviously woody. Even though this

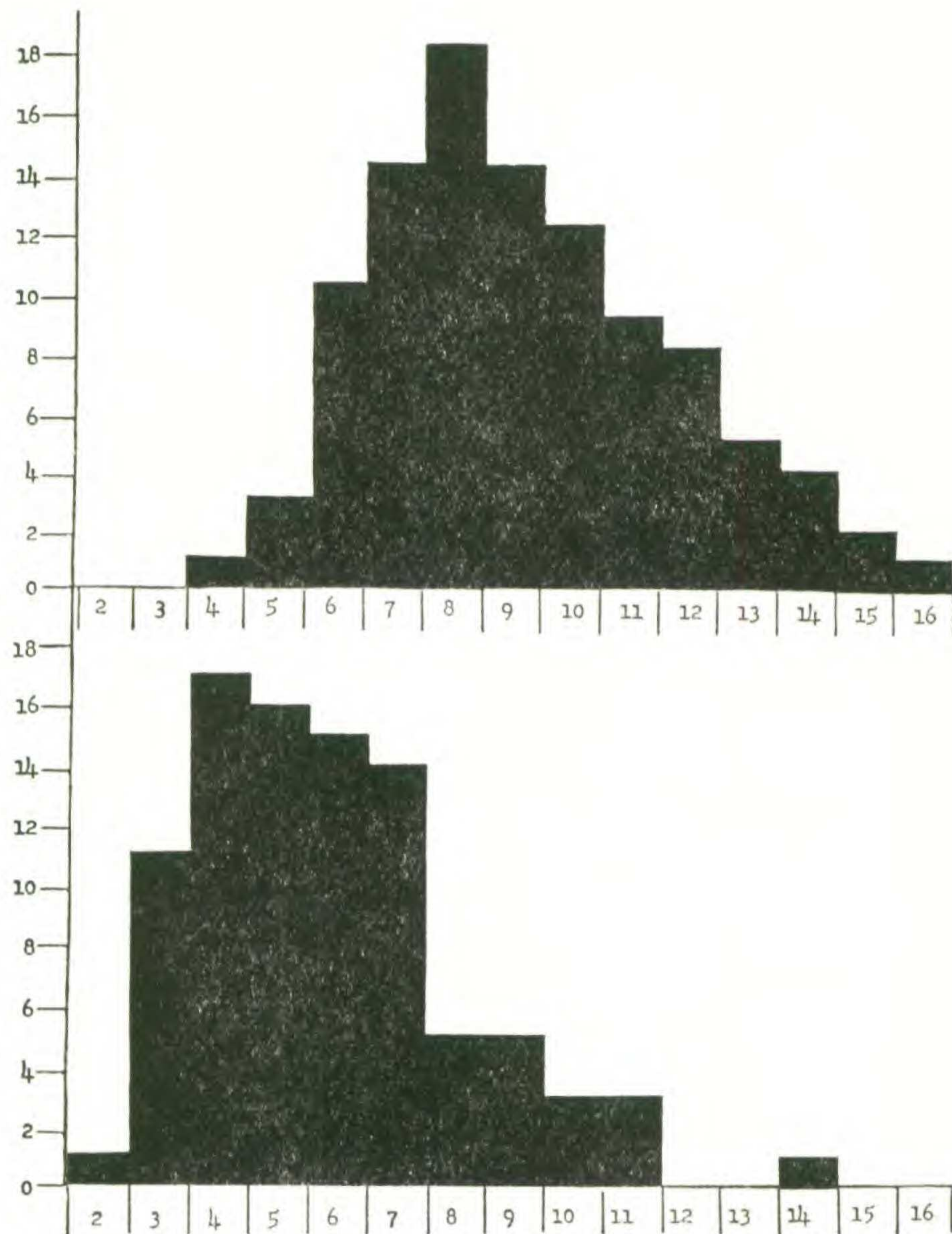


Fig. 5. Length of whip leaf from 100 specimens of *Juniperus virginiana* (above), and 100 specimens of *J. Ashei* (below). Ordinate values represent frequency; abscissae, millimeters.

growth does not represent exactly the same age in each species, the length difference was great enough to render the character valuable. As evidenced by ring transition, a section of *Juniperus Ashei* at any point back from the tip was always slightly older than a comparable point in *J. virginiana*.

In *Juniperus Ashei* the range of variation was from 0 to 200 mm. of terminal whip while the mode was at 40 mm., the median at 60 mm., and the mean at 62 mm. This character was the most variable of all those measured in this species. In *J. virginiana* the range of variation was from 30 mm. to 230 mm. of terminal whip while the mode was 80 mm., the median 120 mm., and the mean 118.8 mm. (See fig. 6.)

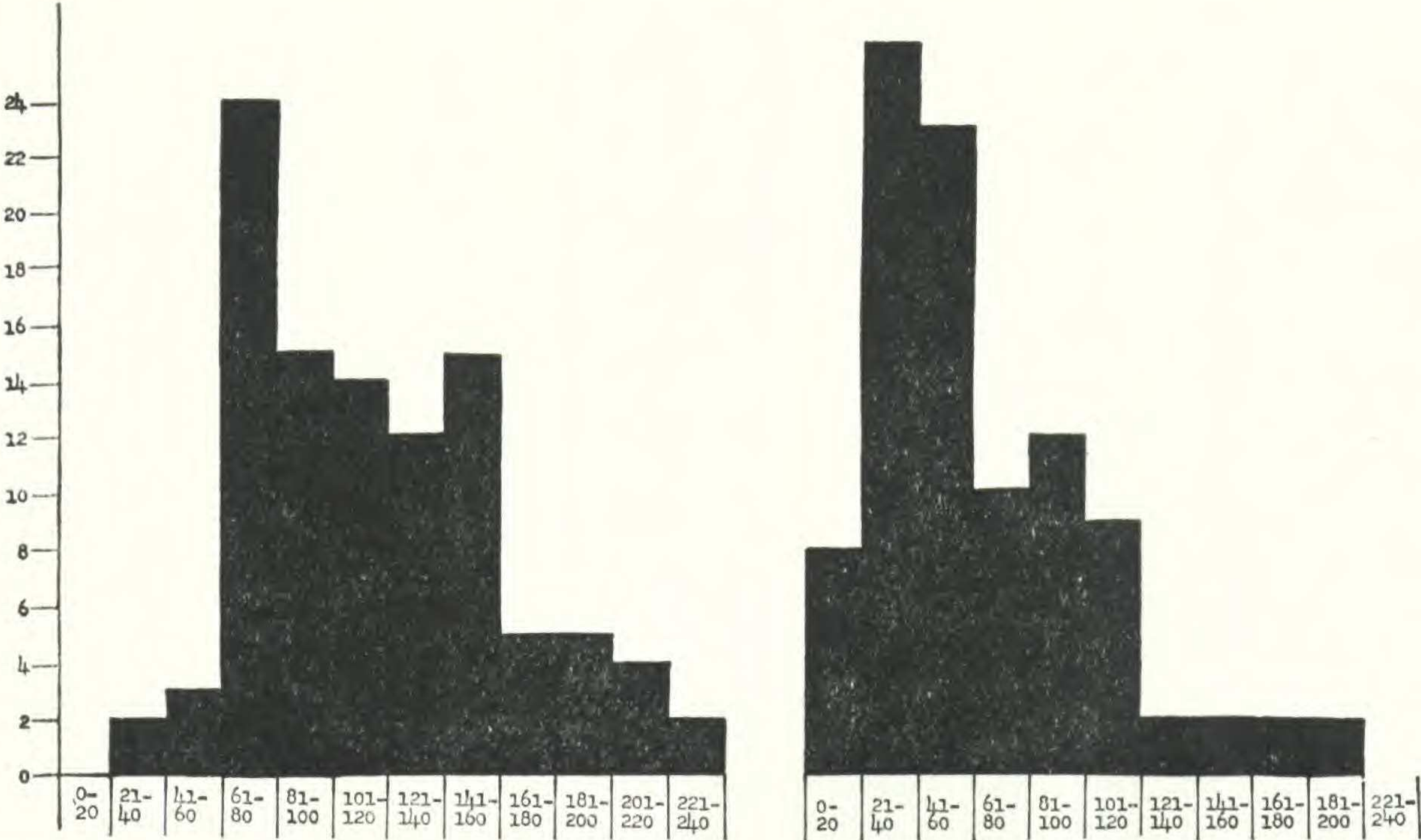


Fig. 6. Length of terminal whip from 100 specimens of *Juniperus virginiana* (left), and from 100 specimens of *J. Ashei* (right). Ordinate values represent frequency; abscissa values, millimeters.

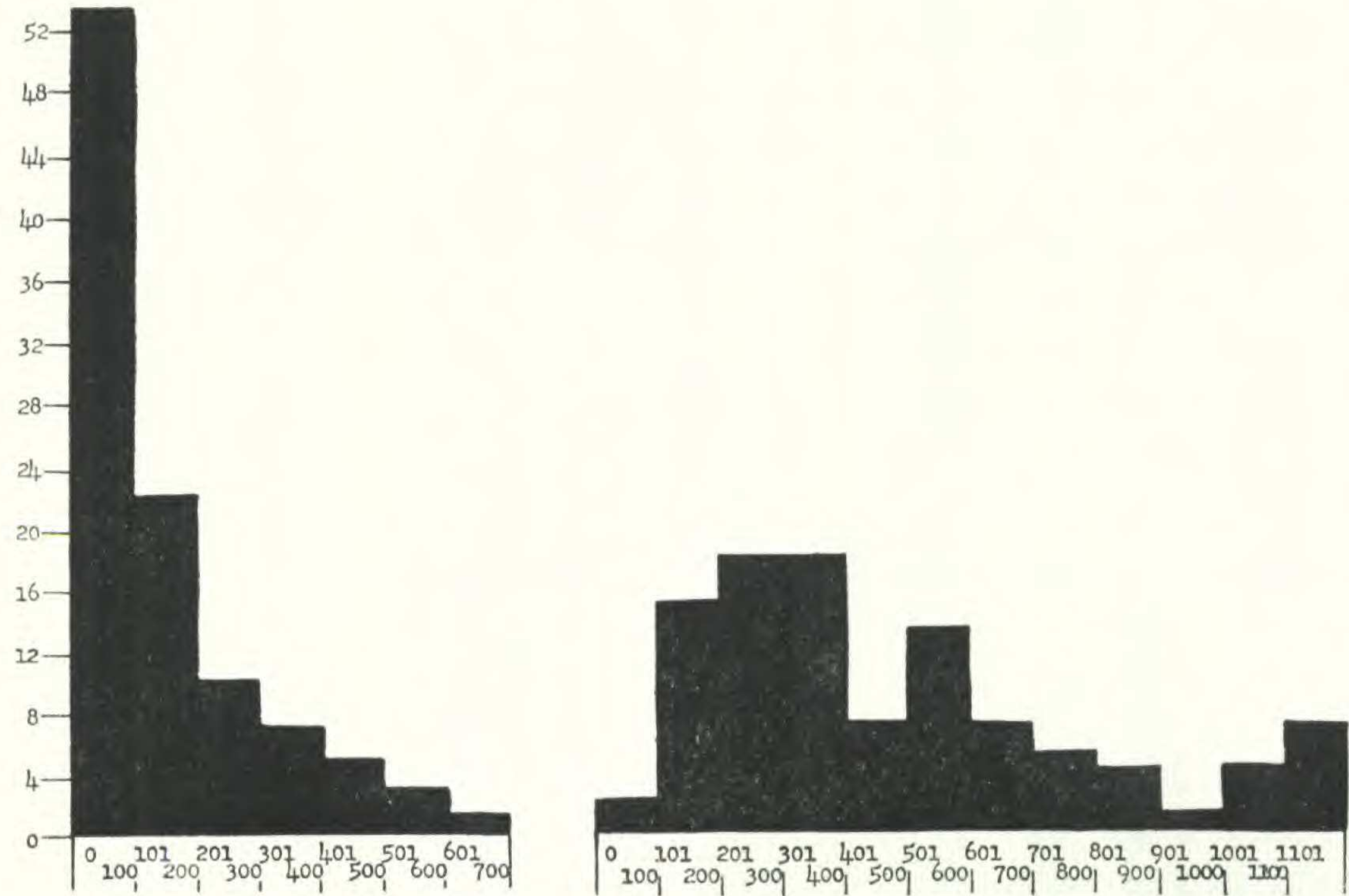


Fig. 7. Length of lateral whip on the secondaries from 100 specimens of *Juniperus Ashei* (left), and from 100 specimens of *J. virginiana* (right). Ordinate values represent frequency; abscissa values, millimeters.

4. LENGTH OF LATERAL WHIP ON THE TERMINAL SHOOT:

This was measured on the same shoots, the secondaries, which bore the terminal whip. These shoots were arbitrarily collected in lengths of 45 cm. The measurements of lateral whip were found to vary from 0 to 1200 mm. With such a tremendous range it was thought advisable to group the measurements, and they were therefore tabulated in units of 100 mm. (fig. 7).

In *Juniperus Ashei* the value with the greatest frequency was 0, the median value was 80 mm., and the mean 90 mm. The range was from 0 to 500 mm. In *J. virginiana* the median value was 410 mm., the mean 390 mm., and the range was from 30 to 1200 mm.

5. PER CENT OF DECUSSATE SPUR SHOOTS ON THE TERMINAL SHOOTS:

This involved the determination of the per cent of the spur shoots on the terminal whip which had leaves in decussate arrangement. Species of *Juniperus* tend to have ternate leaves on the spurs of the terminal whips, but some species have all ternate spurs so situated while others have a variable amount.

Juniperus Ashei typically has the ternate leaf arrangement, as evidenced by the fact that in Group A-I no decussate spurs were found. Groups II, III were not characterized completely by the ternate condition, but instead expressed the trend of increased percentage of the decussate arrangement northeastward. The range in Groups II and III was from 0 to 30 per cent (decussate).

In *Juniperus virginiana* the range of values was from 10 to 100 per cent (decussate); the average as depicted by the median and the mode was 40 per cent; and the mean was 44 per cent (decussate). In this species the spurs on the terminals of an average plant are about one-half ternate and one-half decussate, while in *Juniperus Ashei* they are always ternate except where the two species are in proximity (see fig. 8).

6. LEAF MARGINS:

The SABINA section of *Juniperus* may be separated into two groups on the basis of the presence or absence of teeth on the margins of the leaf. Engelmann (1877) was the first botanist to indicate the value of this character in separating species in the SABINA section, but he admitted that considerable magnification was necessary to render it visible. He wrote, "the edges of the leaf are rarely entire, mostly delicately denticulate, or irregularly fringed with minute, corneous, often curved processes." *Juniperus Ashei* falls into the group with teeth, while *J. virginiana* is in that without teeth. The nature of the margins was discussed in the section on "Comparative Morphology."

From collections represented by Groups A-I, II, III, and Group V, leaves were selected from comparable parts of each specimen and stripped of upper epidermis including the margins. These epidermal peels were stained in aniline blue and mounted in balsam to be studied with respect to marginal dentation. Group A sections displayed the denticulate condition, although an occasional specimen in Groups II and III had fewer teeth than typical, and the cells tended to be situated at a lesser angle to the longitudinal axis of the leaf. In Group V there were no

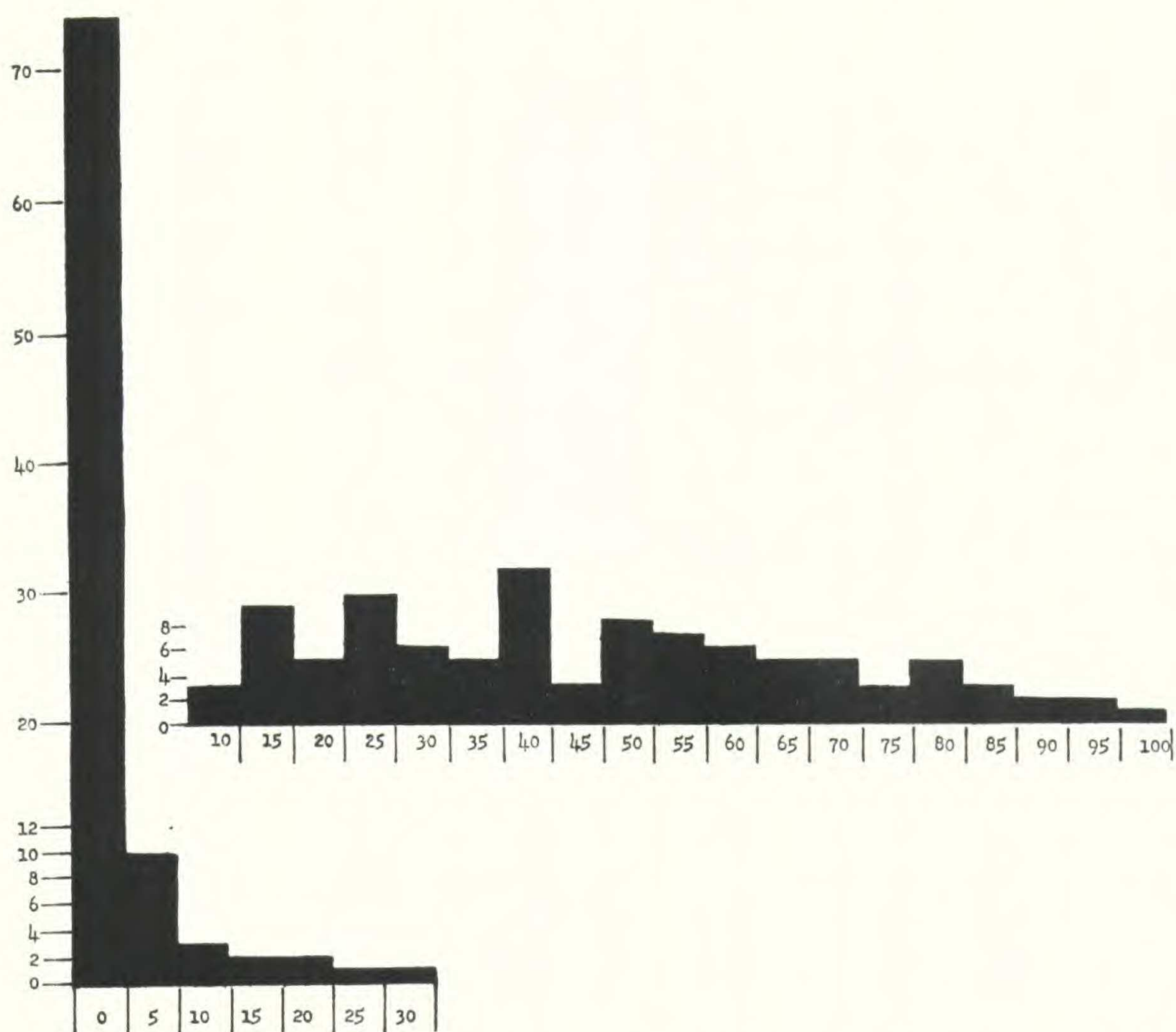


Fig. 8. Per cent of decussate spurs on the secondaries from 100 specimens of *Juniperus Ashei* (left), and from 100 specimens of *J. virginiana* (right). Ordinate values represent frequency.

teeth, and the marginal cells were aligned nearly parallel to the mid-rib. This character was then to be used and scored as D (denticulate), I (intermediate, arbitrarily if 2–4 teeth were visible), S (smooth or entire margins). Then the relative sizes of the epidermal cells of the two species were studied. These data indicated cell size to be a good species difference. There was no overlap in cell size between the two species. *Juniperus Ashei* had appreciably larger epidermal cells which were nearly isodiametric in surface view. The smaller cells of *J. virginiana* were columnar in surface view and nearly always twice or more longer than wide. In some hybrids the cellular pattern was so extremely variable that oddly shaped leaves, which were thought to be a result of upset growth patterns, were common.










VARIABILITY OF THE CHARACTERS

In order to be confident of the index-value of these six characters, it was necessary to learn how much variation might occur in any one of them on a single tree. An intensive study was made on individual plants of *Juniperus Ashei* near Kerr-

ville, Texas, and of *J. virginiana* at the Missouri Botanical Garden Arboretum. This population of Red Cedar was not native material, but of stock brought from Virginia and planted under natural conditions. Intra-individual variation was somewhat less in the southwestern species than in the eastern type of Red Cedar at the Arboretum. In neither example was the degree of variation sufficient to cloud the interpretation of variation of the whole population. Individuals of a bluff population native at the Arboretum were found to show more intra-individual

EXPLANATION OF PICTORIALIZED SCATTER-DIAGRAM SYMBOLS IN FIGS. 9-17

Ordinal character is gland length-width ratio; abscissal character is length of lateral whip.

Whip-leaf length		Per cent decussate	Length of terminal whip
2 - 4		0 - 5	0 - 30
	<i>Ashei</i> -like		
5 - 7		6 - 24	31 - 79
	Intermediate		
8		25 - 100	80
	<i>virginiana</i> - like		

Figs. 9-11. Locations represented by scatter diagrams 1-18, arranged in order of population mean: "Pure" *Juniperus Ashei*, 2-3; "Pure" *J. virginiana*, 8-12. Explanation of symbols above.

Fig. 9—

1. Kerrville, Kerr County, Texas	Population mean 2.13
2. Arbuckle Mountains, Murray County, Oklahoma	2.28
3. Bexar County, Texas	3.72
4. Roaring River State Park, Barry County, Missouri.....	3.96
5. McVey Knob, Ozark County, Missouri	4.12
6. McVey Cliff, Ozark County, Missouri	4.20

Fig. 10—

7. Bald Knob, Taney County, Missouri	4.28
8. Wichita Mountains, Meers, Comanche County, Oklahoma	4.45
9. Austin, Travis County, Texas	4.62
10. Brownbranch, Taney County, Missouri	4.96
11. Lake of the Ozarks, Camden County, Missouri	5.08
12. Fourche a du Clos, Ste. Genevieve County, Missouri	5.16

Fig. 11—

13. Gray Summit Cliff, Franklin County, Missouri	5.20
14. Gray Summit, Cedar Hill, Franklin County, Missouri	5.48
15. Fremont, Nebraska	5.71
16. Nankipoo, Tennessee	5.76
17. Noble, Cleveland County, Oklahoma	6.00
18. Jasper, Newton County, Arkansas	6.00

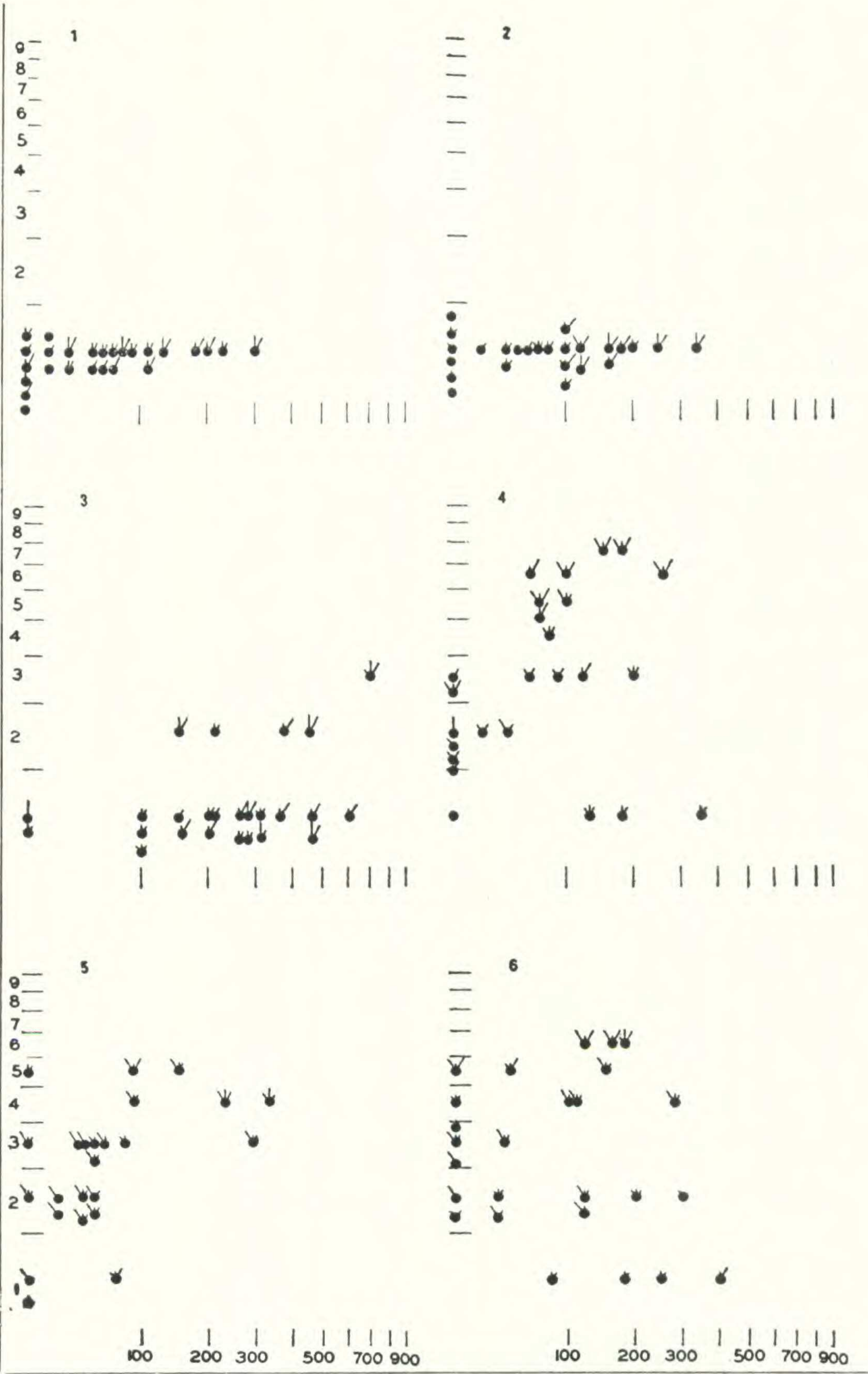


Fig. 9

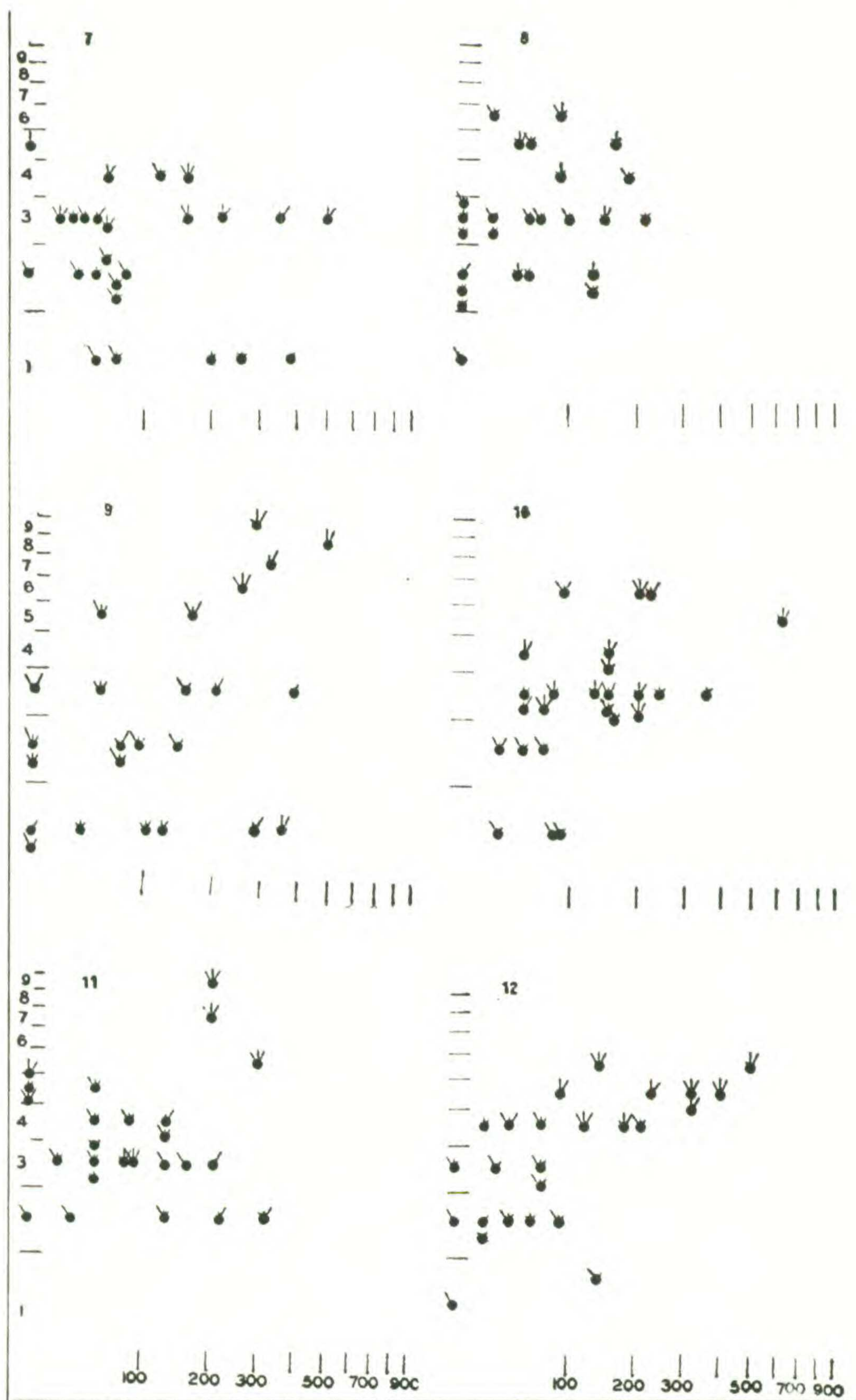


Fig. 10

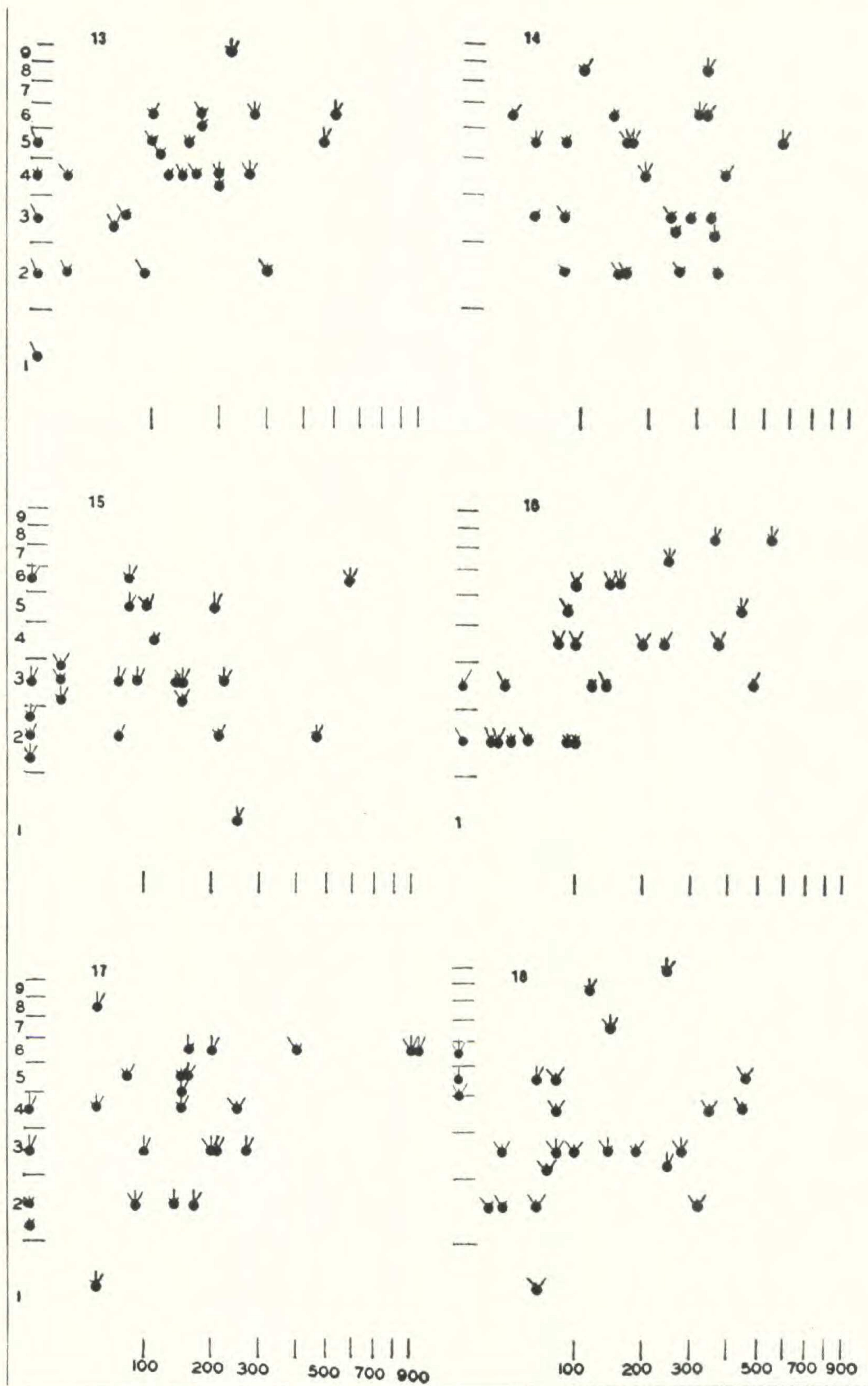


Fig. 11

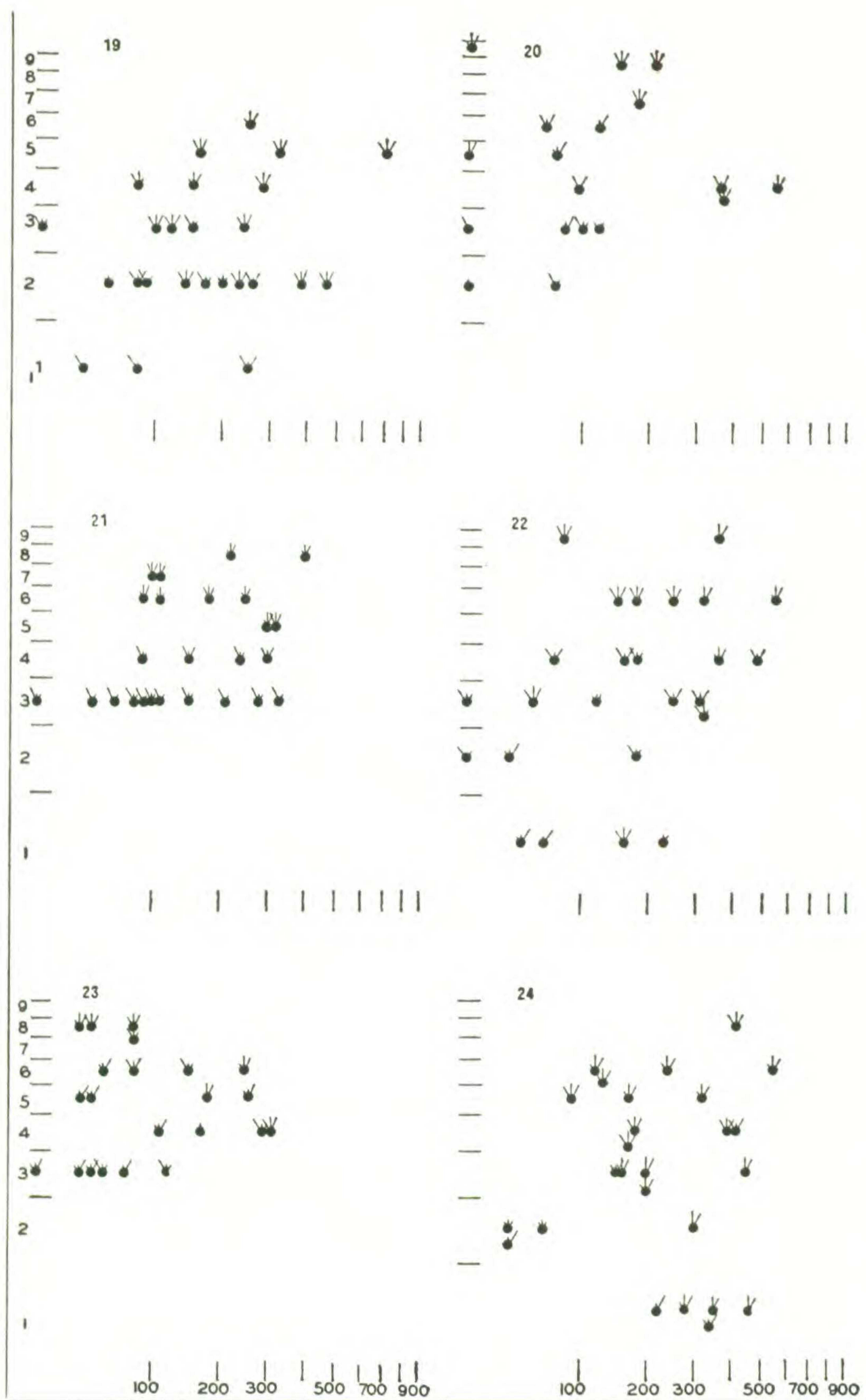


Fig. 12

variation than those from gently sloping hillsides. The variation in these hillside specimens was greater than in bluff populations along the Illinois and the Mississippi rivers.

The variability of individuals of the bluff and glade populations made it necessary to determine the reliability of the methods for recording the intermediacy and the variability of whole populations. By actual test it was found that the methods gave repeatable results and were therefore scientifically valid. Repeated scorings of labelled populations gave the same general population picture, even though the values for individual trees were not always precisely the same in each diagram. Repeated samplings of the same population by one individual, or independent samplings by two observers, produced essentially similar population diagrams.

The program was complicated by the great intra-individual variability of certain of the specimens, particularly those in the areas of intensive introgression. Though the phenomenon has never received critical study it is well known to various students of hybridization that hybrids, both in artificial and natural populations, may have greater intra-individual variation as well as the greater inter-individual variation which is known to be so characteristic. It might be argued that this greater lability of the Ozark trees was the result of the environment in which they were growing. In answer to this, one might point to the Ashe Junipers themselves. Though growing in an environment which is similar to the Ozark

Figs. 12-14. Locations represented by scatter diagrams 19-36, arranged in order of population mean: "Pure" *Juniperus Ashei*, 2-3; "Pure" *J. virginiana*, 8-12. Explanation of symbols on page 40.

Fig. 12—

19. Arpelar, Pittsburg County, Oklahoma.....	Population mean 6.04
20. Indian Springs, Crawford County, Missouri	6.10
21. Olivehill, Carter County, Tennessee	6.16
22. Wilburton, Latimer County, Oklahoma	6.20
23. Caddo Canyon rim, Caddo County, Oklahoma	6.24
24. Platt National Park, Murray County, Oklahoma	6.31

Fig. 13—

25. Poteau, LeFlore County, Oklahoma	6.36
26. Pilot Grove, Iowa	6.40
27. Scott County, Missouri	6.52
28. Ludwig, Johnson County, Arkansas	6.64
29. Talihina, LeFlore County, Oklahoma	6.84
30. Columbus, Kansas	7.13

Fig. 14—

31. Mt. Pleasant, Iowa	7.15
32. La Grange, Lewis County, Missouri	7.20
33. Butts, Crawford County, Missouri	7.32
34. Paducah, McCracken County, Kentucky	7.34
35. Raleigh, Wake County, North Carolina	7.44
36. Rosedale, Jersey County, Illinois	7.60

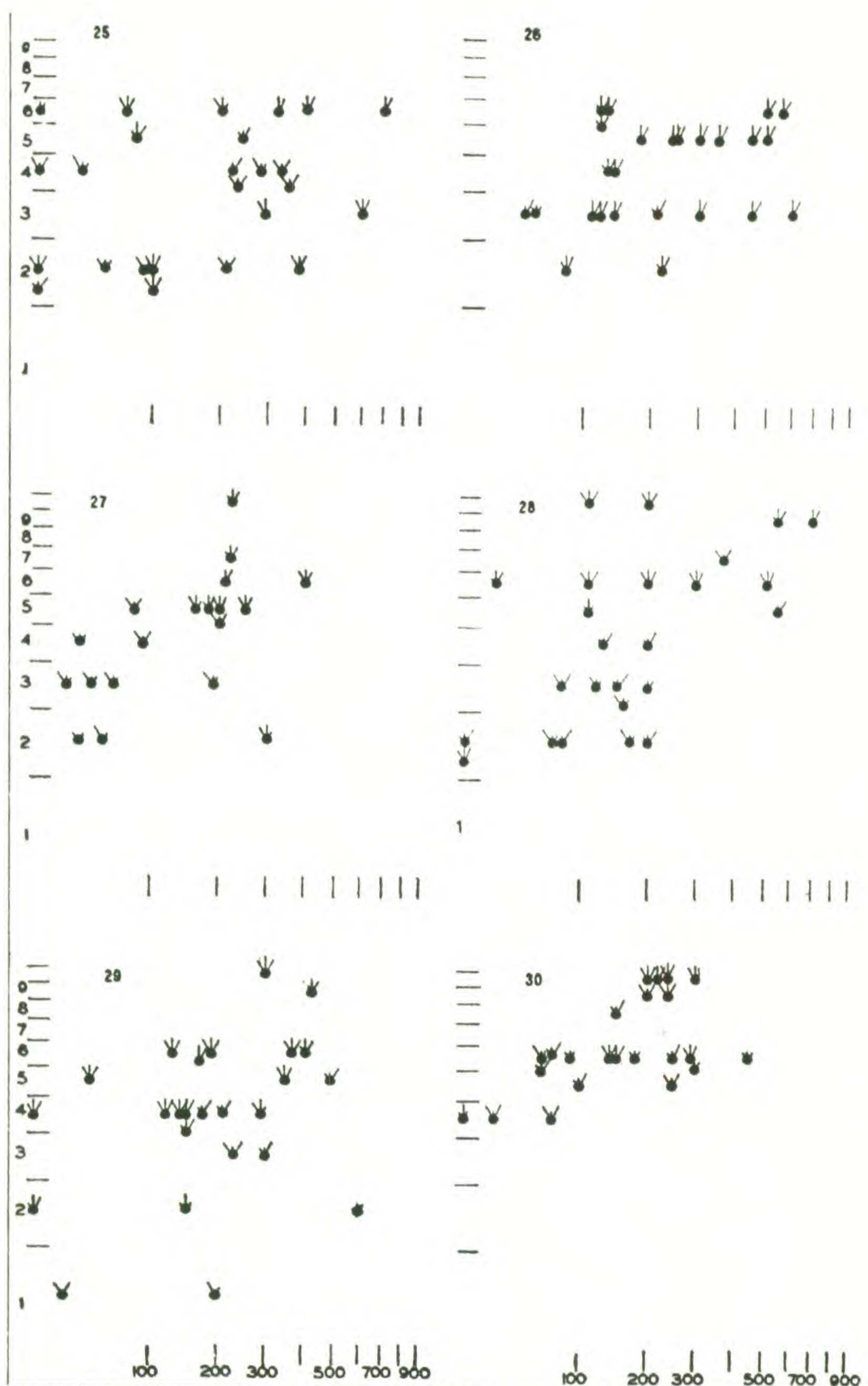


Fig. 13

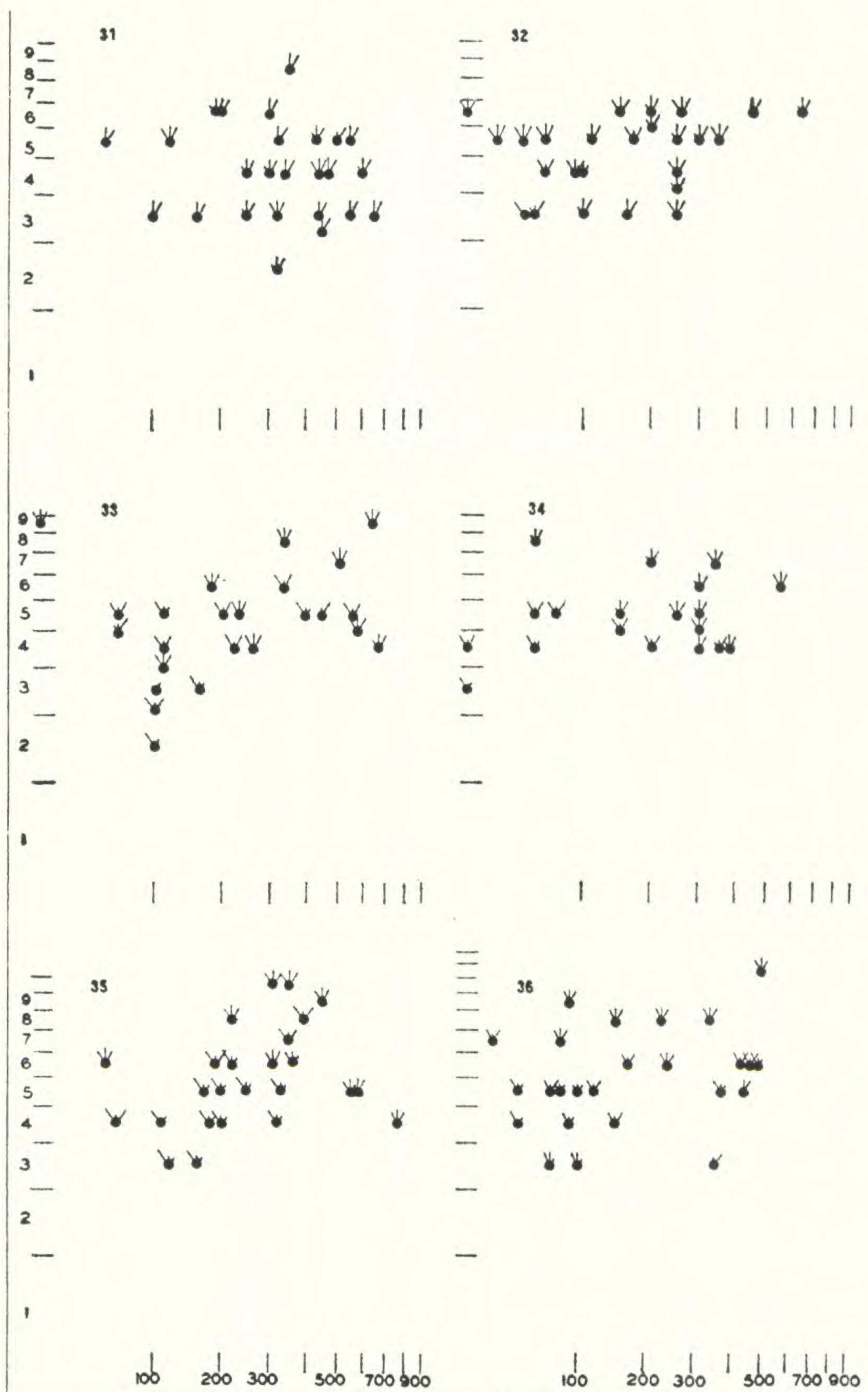


Fig. 14

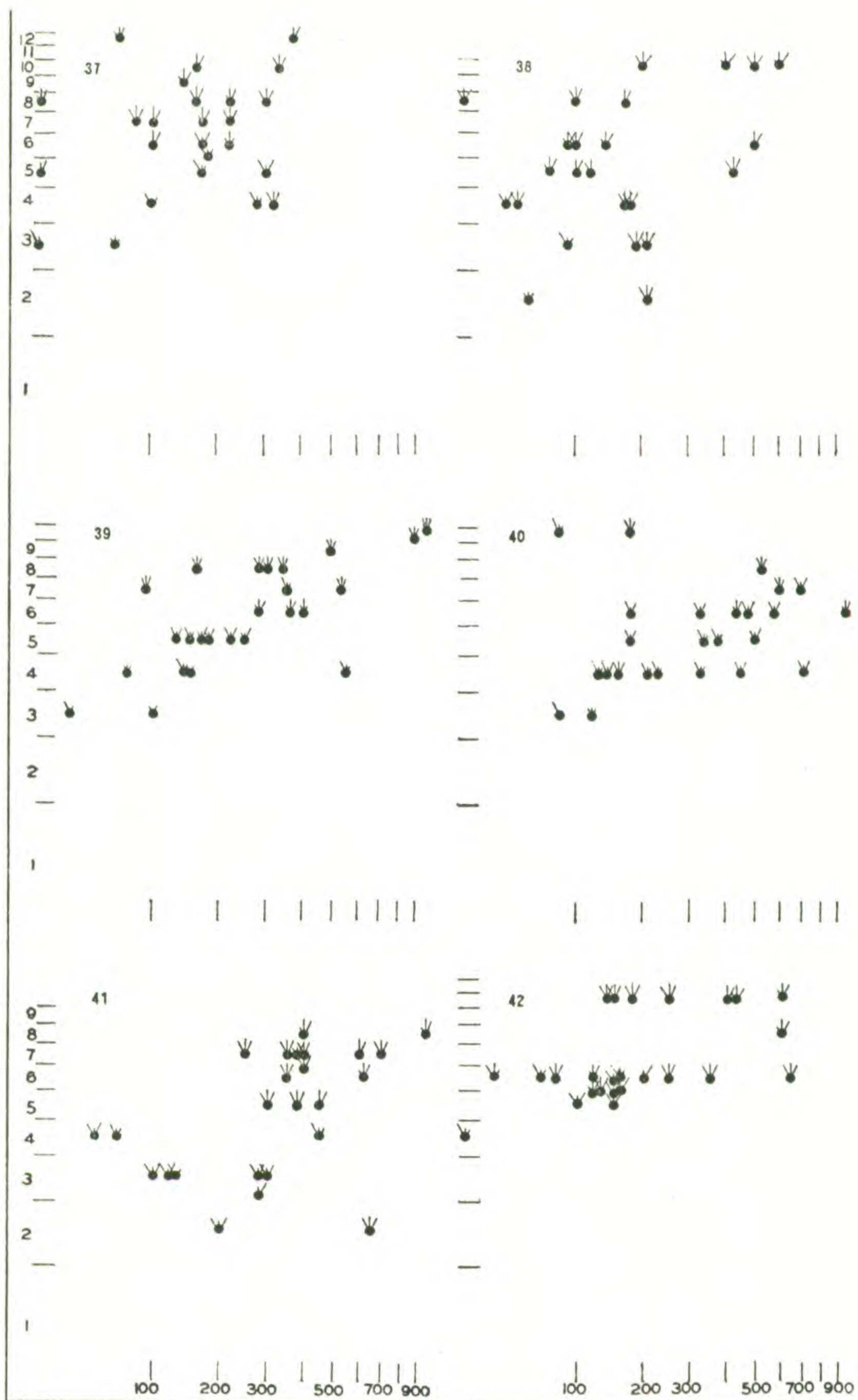


Fig. 15

glades and bluffs, the "pure" Ashe Junipers exhibit no more intra-individual variability than do the "pure" specimens of Red Cedar from Tennessee. In other words, the variability patterns of the Ozark junipers do not follow a logical development in terms of the influence of environment alone. When all the data are integrated and juxtaposed on their geographical backgrounds, it is obvious that the mixing of germ-plasms plays the important role in determining the heterogeneous nature and the biotypic differentiation of Red Cedar in the Ozark region and southwestward.

To check the effect of environment, climate particularly, a study was made of *Juniperus virginiana* var. *Canaertii* from Oklahoma to eastern Michigan. This variety is usually propagated by grafting young seedlings onto native Red Cedar stock. A population at the University of Oklahoma Nursery in Norman was scored, one in St. Louis, Mo., and one in Ann Arbor, Mich. The scatter diagrams (fig. 17, Populations 52, 53, 54, composed of individuals grafted onto root systems of local Red Cedar stock) illustrate the extreme homogeneity. However, specimens were also scored which were grafts onto Chinese Arborvitae (*Thuja orientalis*) root systems. These pictograms were identical with the ones illustrated. It would be wrong to assume that only one horticultural variety should be an index to environmental effects on the species, but several well-known varieties were carefully examined in nurseries and arboretums in order to satisfy that point.

POPULATION STUDY

The patterns of these six characters having been found to be suitable indications of specific affinity without too much clouding through environmental modifications, population sampling was undertaken on a large scale. The minimum number of 25 specimens to be studied per population was set for two reasons: (1) The diagrams for 25 specimens studied at the Missouri Botanical Garden Arboretum produced the same picture as those for 50 specimens; (2) The paucity of mature specimens in a few areas (regions where a very high percentage of the land was under cultivation) necessitated the utilization of reasonably small samples.

During this phase of the study, specimens from 54 populations, representing 1,350 individuals, were measured for the six characters listed; sex and berry diameter were recorded; and the habitat was briefly described. These data and mass collections from all these areas are filed at Cranbrook Institute of Science, Bloomfield Hills, Mich. The specimens were collected in the area from Virginia

Fig. 15—

37. Wichita Mountains, Mt. Scott, Comanche County, Oklahoma.....	Population mean 7.60
38. Caddo Canyon floor, Caddo County, Oklahoma	7.70
39. Spring Hill, Maury County, Tennessee	7.76
40. Baker's Grove, Davidson County, Tennessee	7.80
41. Carbondale, Williamson County, Illinois	8.20
42. Craig County, Virginia	8.30

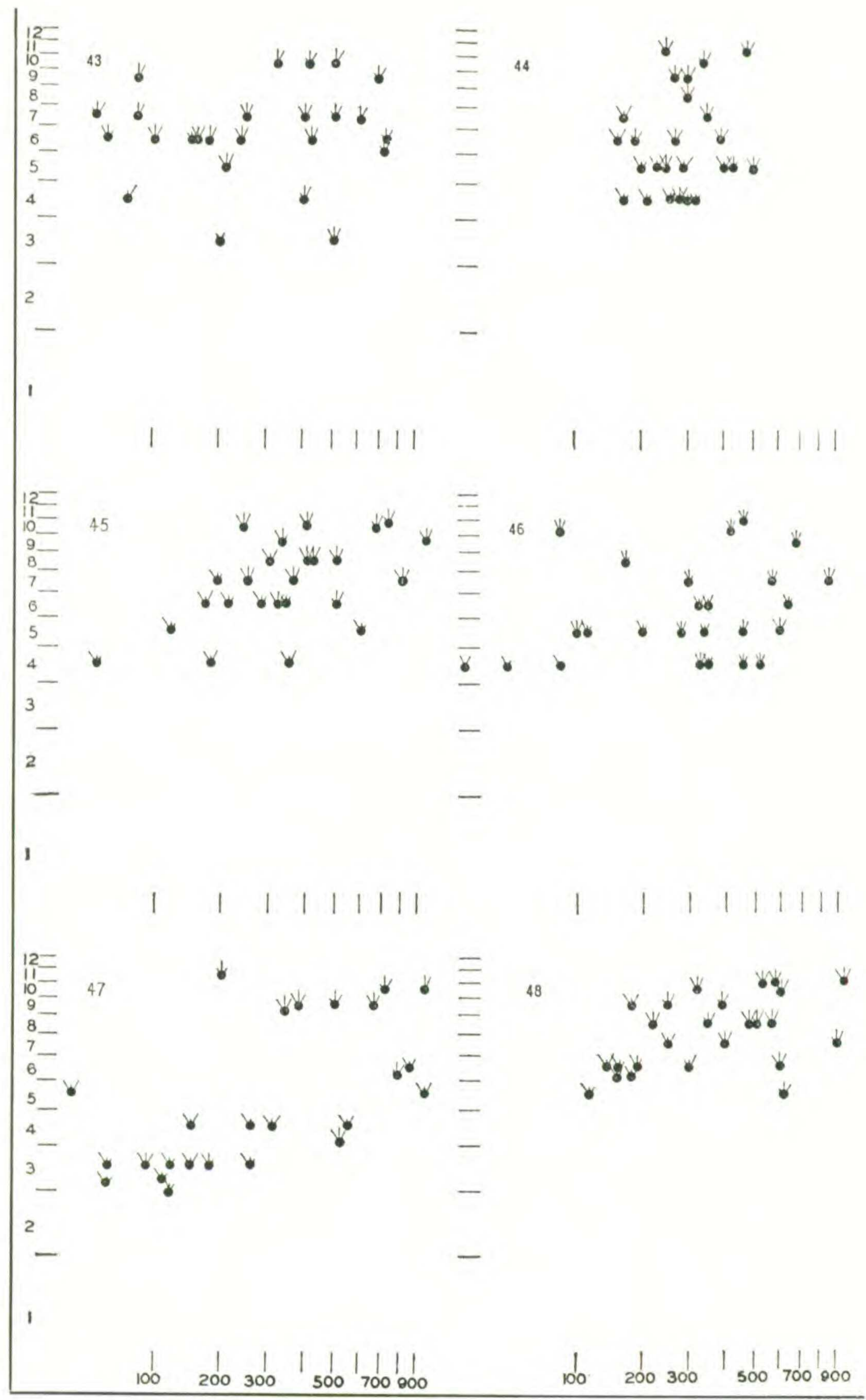


Fig. 16

to North Carolina and west to Nebraska and southern Texas. Some specimens outside this area were studied—southwestern New York state, southern Michigan, and the Atlantic Coastal region. Areas where *Juniperus virginiana* meets *Juniperus horizontalis* or *Juniperus communis* were not studied in detail.

Pictorialized scatter diagrams (Anderson, 1949) of each population were plotted on a log-log scale, but normal values for the characters were used. This technique was used chiefly to keep the populations on a single sheet. The log plots condense the high values and spread the low ones, effecting a diagram which displays the relative degree of variability very successfully.

In making up the scatter diagrams, all the six characters were used except that of leaf margin. The five characters were plotted, using different combinations of them for the abscissa and ordinate. In each case, even though the position of individual specimens varied somewhat, the total plot remained very nearly the same. However, it seemed most sensible to use either the characters with the greatest range or the greatest absolute difference; therefore, along the abscissa were plotted values for lateral whip and along the ordinate values for ratio of gland length to width. The data for the other three characters, per cent decussate foliage, length of whip leaf, and length of lateral whip, were grouped into three classes: (1) plants in which the measurements for each single character were *Ashei*-like, (2) *virginiana*-like, or (3), intermediate. *Ashei*-like characters had low values and were designated by a black dot; *virginiana*-like ones had high values and were designated by a dot with long rays; intermediate ones were designated by a dot with short rays. The legend on page 40 gives an explanation of the pictorialized scatter-diagram symbols.

Figure 18 is a pictorialized scatter diagram of a typical population of *Juniperus Ashei* (shown as squares) from the Edwards Plateau; of *J. virginiana* (shown as dots) from the Interior Low Plateaus; and of intermediates (shown as squares with superimposed dots) from Oklahoma and Missouri. This diagram is the heart

Figs. 16–17. Locations represented by scatter diagrams 43–54, arranged in order of population mean: "Pure" *Juniperus Ashei*, 2–3; "Pure" *J. virginiana*, 8–12. Explanation of symbols on page 40.

Fig. 16—

43. Wichita Mountains, Cache, Comanche County, Oklahoma.....	Population mean	8.50
44. Lebanon, Wilson County, Tennessee		8.56
45. Fritchton, Knox County, Indiana		8.85
46. Sumner County, Tennessee, near state line		8.96
47. Harrisville, Arkansas		8.96
48. Hadley, Warren County, Kentucky		9.00

Fig. 17—

49. Eudora, DeSoto County, Mississippi		9.36
50. Ninevah, Virginia		9.85
51. Warm Springs, Virginia		10.80
52. St. Louis, Missouri, Goetz Nursery. <i>J. virginiana</i> var. <i>Canaertii</i>		10.00
53. Norman, Oklahoma, University Nursery. <i>J. virginiana</i> var. <i>Canaertii</i>		10.03
54. Ann Arbor, Michigan, Ann Arbor Nursery. <i>J. virginiana</i> var. <i>Canaertii</i>		10.04

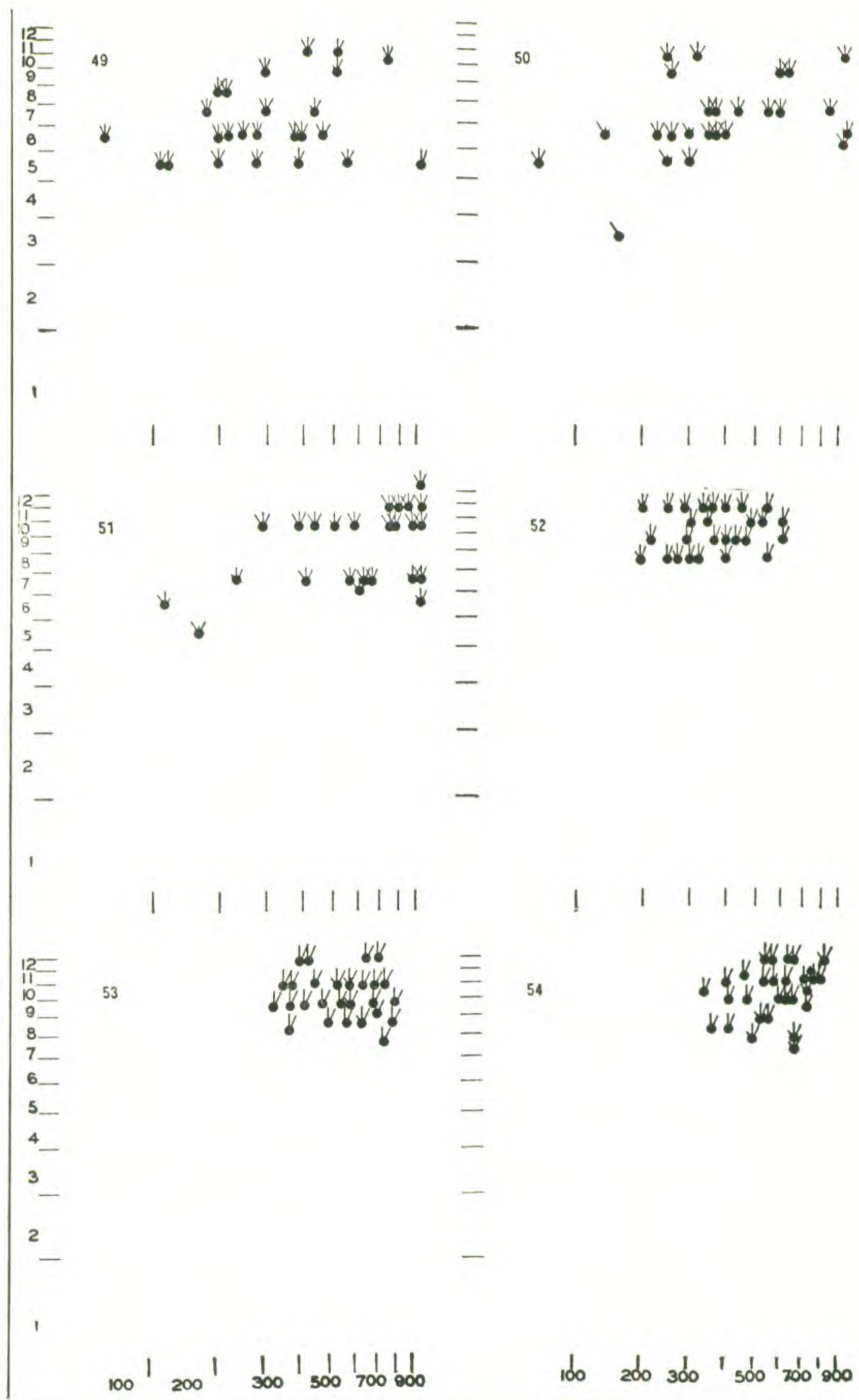


Fig. 17

of the study and demonstrates several important points: (1). The pattern of the recombinations is typical of interspecific crosses. The "recombination spindle" is fairly wide, suggesting that either the linkage is not exceptionally strong or else the natural plasticity of the characters is responsible for widening the "spindle." (2). No combinations occur which may be described as reciprocals. (3). The characters from each species tend to stay together in the intermediates, suggesting linkage. (4). More of the intermediates overlap or tend toward the characters of *Juniperus virginiana* than *J. Ashei*, which is probably the result of either differential introgression or differential selection of introgressants.

The data from the scatter diagrams were grouped to obtain a mean index value for each population. The coordinate positions were assigned values by means of a grid which divided the diagram into equivalent units from 0 (lower left of diagram) to 10 (upper right of diagram). The symbols were evaluated as follows: dot, 0; dot with short rays, 1; dot with long rays, 2. For any individual's index, its values were added to its coordinate position value. These were totaled for the whole population and divided by the number of individuals to obtain the mean index for the population. These grouped-data means corresponded closely to the population means obtained from the original measurements. This method was used because of the speed as well as the accuracy with which the populations could be typified. Obviously, these grouped data tend to obscure the differences within the populations of intermediates.

Map 2 uses the index values to indicate the character of the populations in their geographic setting. This map clearly indicates the geographic differentiation of *Juniperus virginiana* in relation to introgressive hybridization with *Juniperus Ashei*.

GEOGRAPHIC RACES OF *Juniperus virginiana*

Two races may be differentiated within the species *Juniperus virginiana* as a result of this study. They are here named *Typica* and *Ozark*.

Typica (area 1 on Map 3) is composed of two habitat forms which vary concordantly and have been known for some time by horticulturists as Eastern and Tennessee. Briefly, the Eastern form is the very tall, narrowly pyramidal tree which reaches its best development in the Appalachian Plateaus. Populations of the Eastern form have an index value from 9 to 10. This form is also found in the Central Lowlands as far west as the Shawnee Hills and throughout the Interior Low Plateaus. The Eastern form has an associated habitat form within part of its range with which it is morphologically concordant (Anderson, 1949). This more xeric form, known as Tennessee, is the slower-growing, smaller, straight-trunked, glade plant whose lowermost lateral branches are close to the ground even in old specimens. The Tennessee, which appears to be a diminutive of the Eastern, has index values from 7.5 to 9.0. This form is characteristic of the limestone glades (barrens) of the Interior Low Plateaus and may frequently be found growing near the eastern form but always in the most xeric habitats of the locale. The Tennessee form is best developed on the Lebanon limestone of the Nashville Basin.

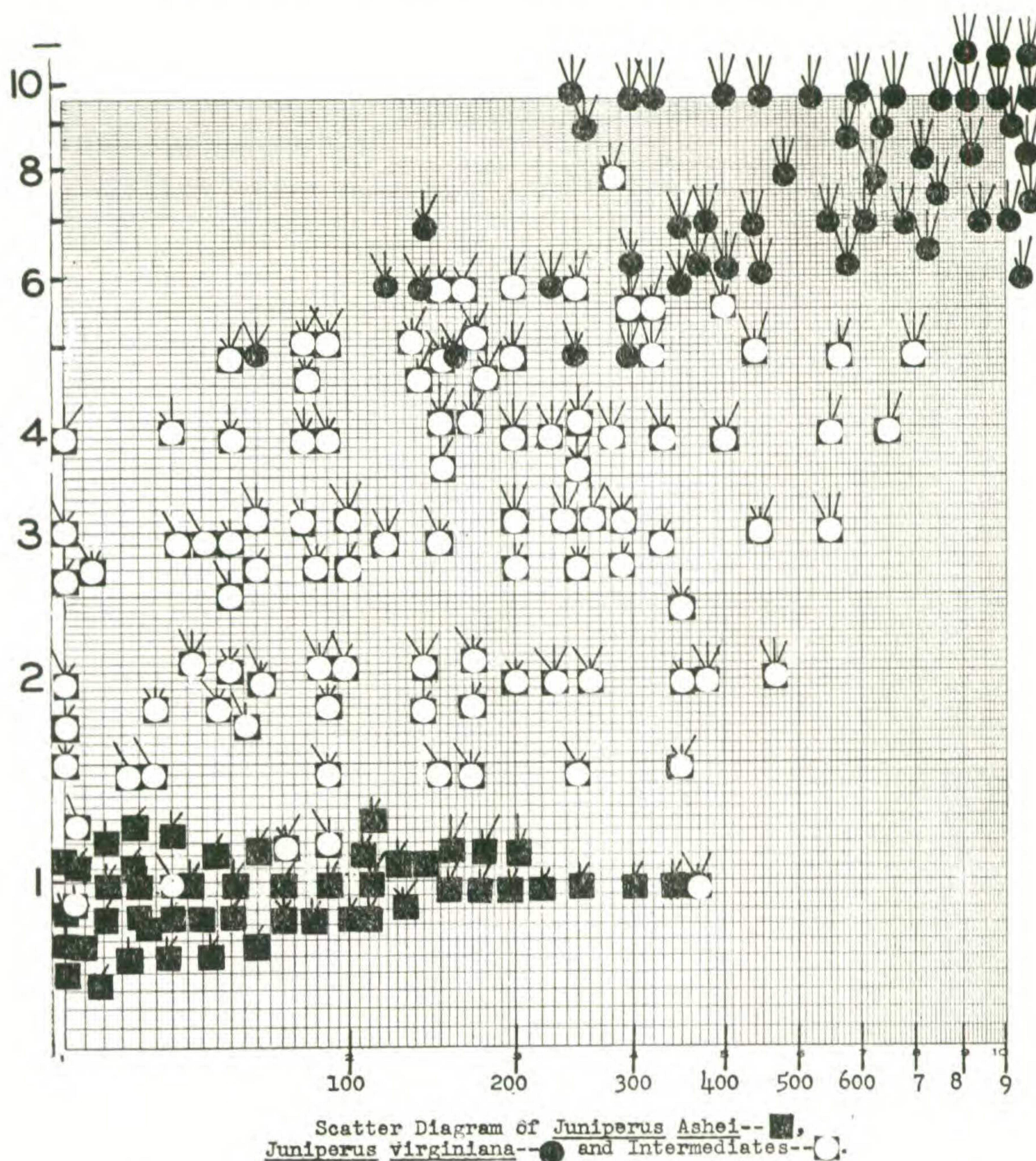
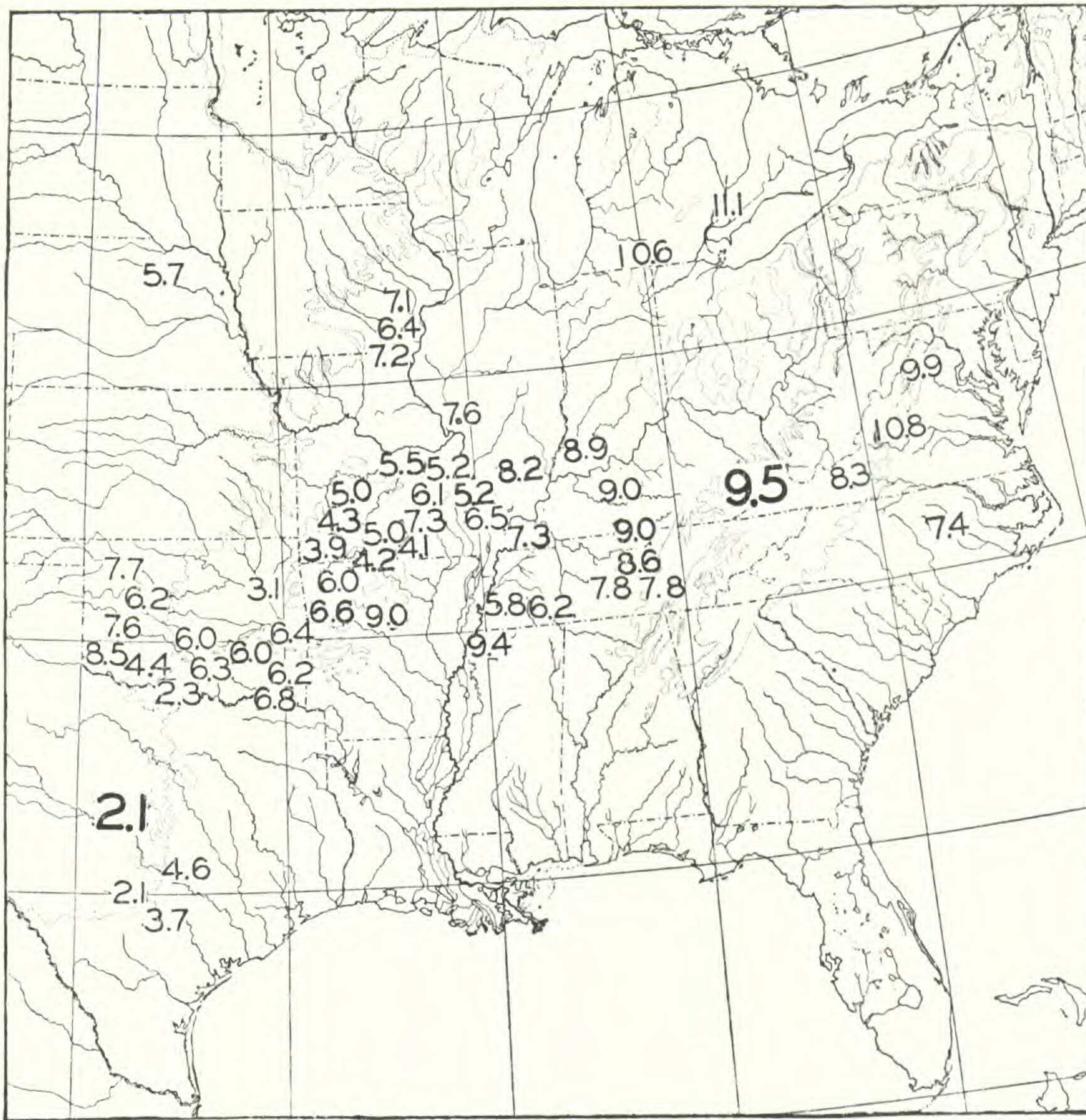


Fig. 18. Scatter diagram of *Juniperus Ashei*, *J. virginiana*, and intermediates represented by 200 individuals: 50 specimens of *J. Ashei* from the Edwards Plateau, 50 specimens of *J. virginiana* from the Interior Low Plateaus, and 100 intermediates from Oklahoma and Missouri. Gland length-width ratio is plotted on the ordinate; length of lateral whip on the abscissa. The bar values are the same as given for the diagrams (figs. 9-17) on page 40.

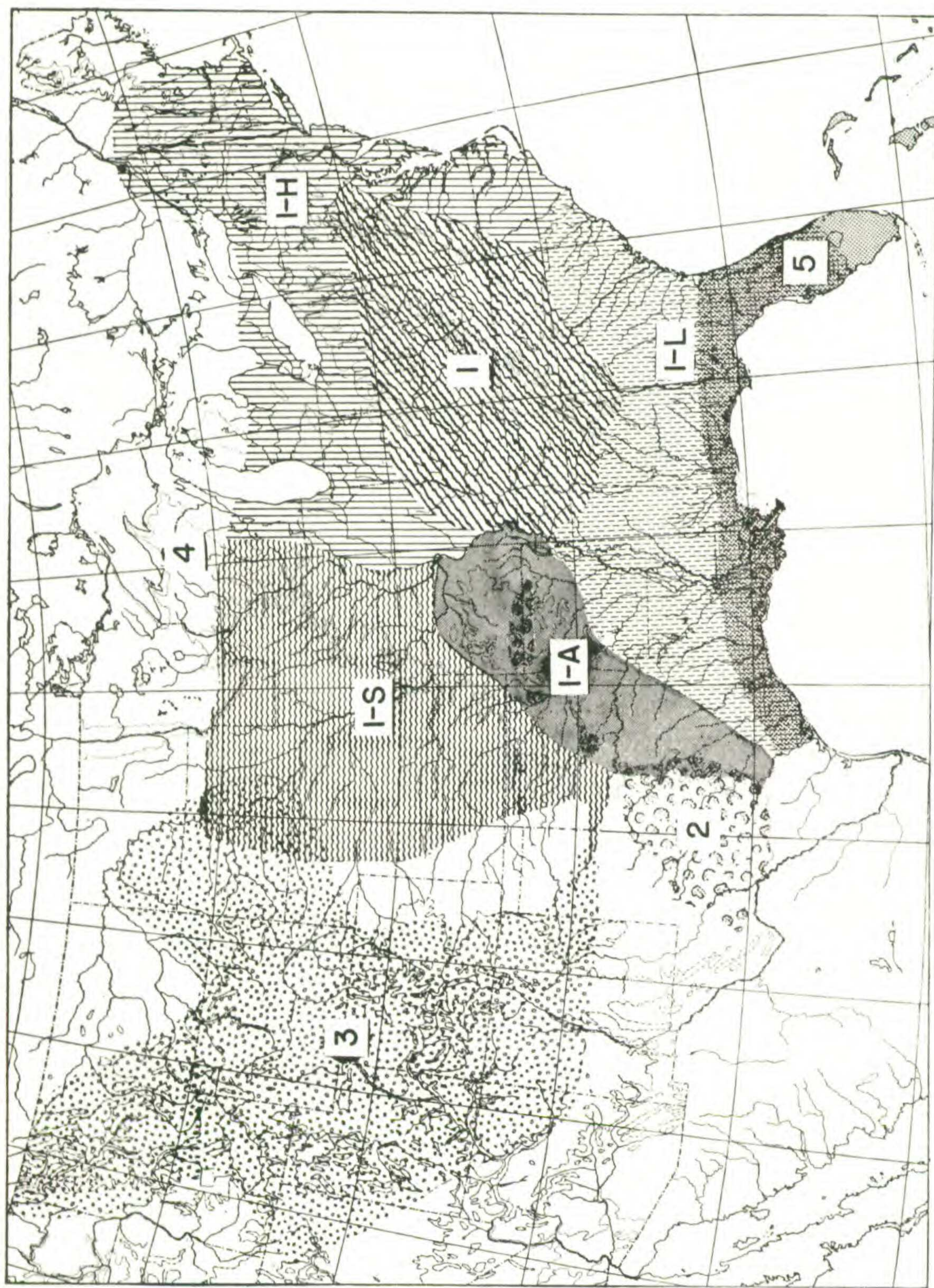
The Ozark race (area 1-A of Map 3) includes a most heterogeneous assemblage with index values ranging from 4 to 7. Populations which score approximately 4 are all hybrid swarms on limestone, usually dolomitic, knobs or glades made up of individuals with characters of either species. However, the index value of swarms may vary according to the ability of *Ashei* and *Ashei*-like individuals to survive in the habitat. The hybrid swarm at Platt National Park, Oklahoma, had an index of 6.3. The area is in the Oak-Hickory savannah (Bruner, 1931) but is open and covered with a dense stand of *Andropogon scoparius*. The soil originates from the



Map 2

The geographic distribution of population means for 54 populations (plotted to the nearest tenth).

calcareous Pontotoc Conglomerate. The water table is near the surface, so that this particular site, which is not well drained, is a somewhat unfavorable habitat for *Juniperus Ashei* and its putative relatives. The hybrid swarms of the bald knobs in southwestern Missouri are in much more xeric environments—dry limestone knobs with thin rocky soil formed by erosion of the Burlington limestone. This limestone occurs in flat layers (giving the effect of laminated terraces) which are relatively impervious and, except where the slope is steep, do not drain too well. Likewise, ground water does not readily find its way back into the soil above the layered rock. Thus, these areas are wet in early spring but very dry in summer and fall. The tops of the knobs and the southwest slopes are favorable habitats for *Juniperus Ashei*, while the rest of the area is thickly populated with the introgressants; hence the low per cent of *Ashei* at Platt and the high per cent on the knobs. Populations which score 5 are situated on bluffs or glades. Those with



Map 3

Distribution of species: Area 1 (and 1-A, 1-B (1-L on map), 1-H, 1-S), *Juniperus virginiana*; Area 2, *J. Asbei*; Area 3, *J. scopulorum*; Area 4, *J. horizontalis*; Area 5, *J. barbadensis*.

Distribution of introgressants of *J. virginiana*: Area 1-A, Ozark race (*J. Asbei*); Area 1-B (1-L), Florida race (*J. barbadensis*); Area 1-H, Northern race (*J. horizontalis*); Area 1-S, Platte River race (*J. scopulorum*).

score 6 are similar to *Typica*, and in the Ozarks they grow in open woods, prairies, and along creeks and rivers. They are much more heterogeneous (discordantly varying) than *Typica*.

The evidence indicates that the Ozark race with all its heterogeneous forms is a product of the mixing of the southwestern species, at times past and to some extent at present, with the eastern species and the subsequent selection of gene combinations distributed by birds, water, mammals, and man. The strength of the evidence is morphological and lies in the presence of combinations of characters of the two species of the Ozark Highland and the Southwest. These combinations of characters mostly have their replicas in the hybrid swarms and from them spread many miles and along many lines of selection.

DISCUSSION

The problem presented in this paper is merely one portion of the problem of variability in *Juniperus virginiana*. It deals with the effect of hybridization and introgression between *Juniperus Ashei* and *J. virginiana*. Each species is influenced by other species not included in this study: *J. Ashei* where it meets *J. Pinchotii* and *J. monosperma*; and *J. virginiana* where it meets *J. horizontalis*, *J. scopulorum*, and others.

The index map (Map 2) shows the apparent extent of influence of *Juniperus Ashei* on *J. virginiana*. This influence is measurable only in the Ozark Highland and southwestward, and in the South perhaps as far as the Tennessee River. Populations of *J. virginiana* with means from 4 to 7, whether mixed or not with actual specimens of *J. Ashei*, still show influence of the germ-plasm of the southwestern species. The criteria are morphological and based on combinations of characters from each species.

The population mean does not give a very good picture of the individuals which make it up (compare the scatter diagrams for populations 23, 24, 25). For example, in the Caddo Canyon (23) population the influence of *Juniperus Ashei* is only slight as compared to that in the Platt National Park (24). The same holds for the Poteau population (25). In the Platt National Park there are greater and more frequent extremes, but the mean is practically the same. Yet, the more homogeneous populations still show characters of each species. The most conspicuous differences among the three populations are in the habitats.

The canyon rim population from Caddo Canyon is in the tall-grass prairie above the deep canyons of Sugar Maple forest. The canyon vegetation is classed as a post-climax deciduous forest relic (Little, 1939). There is abundant massive red sandstone (Whitehorse formation) which has permitted the Washita and South Canadian Rivers to cut deep canyons into the ridge separating their flood-plains. Cedar-brakes and tongues of short Post Oak-Black Jack Oak savannah frequently follow the creeks into the tall-grass prairie. The annual rainfall is approximately

30 inches. Junipers on the rim show obvious affinities to *Juniperus Ashei*: some are bushy; others have very long up-turned basal branches; still others have slightly toothed leaves which under a compound microscope show the characteristic hooked cells. They have larger fruit than does typical *J. virginiana*, but there are no real extremes in either direction. The area is not suitable for the calciphilous southwestern species and its extreme recombinations. There are present only the less dramatic intermediates. On the canyon floor, 100 feet below, *J. virginiana* is entirely different and shows obvious affinities to *Juniperus scopulorum*, not *J. Ashei*.

The Poteau, Oklahoma, population is growing on the resistant sandstone bluffs and banks of the Poteau River which flows in the Arkansas Valley Province in the Oak-Hickory savannah vegetation zone. Even though the average annual rainfall is 44 inches, the coarse porous sandstone and steep banks of the river insure rapid drainage, and the open savannah country permits high transpiration. Since the area is not suitable for the extremes of *Juniperus Ashei*, it is not surprising to find intermediates, not of a striking nature, but homogeneous enough to give a mean corresponding to that of the hybrid swarm of Platt National Park.

It is most important to realize that the habitats of *Juniperus* can be roughly defined more efficiently by a mass collection than by the various paraphernalia for measuring physical factors of the environment. This is possible only after one has gained knowledge of and experience with the organisms in question. This generalization holds only for introgressing species which have distinctive ecological differences. The heightened variability is made possible through extensive long-term hybridization, possibly discontinuous in time, from which various environments along the way have selected those plants able to establish and reproduce themselves. This is a dynamic process and demonstrates that just as individuals and species are constantly changing, often in multi-faceted ways, so also are the colony, the community, and the association; thus, here is the accentuation of Cooper's (1926) classic expression, that so-called climax formations are only "variables approaching a variable," a continuum.

Population studies are valuable to the ecologist, since they shed light on the relations of the taxons, the environment, and natural selection. It is a problem of "workman know your tools." The ecological potentials of the partially discontinuous genotypes making up the species complex or complexes, even though not precisely known, are predictable on a considerably better basis than guesswork. Such complex populations with no absolute internal discontinuities are bound to have almost inexplicably complex ecological patterns. Such species have great survival value in the face of changing environments.

Ecotypic differentiation must be greatly accelerated following introgression, especially if the ecological requirements of the introgressants are relatively different. It is quite likely that mixing of germ-plasm is responsible for the wide range of distribution of *Juniperus virginiana*. Reference to Map 3 will show the

feasibility of such an hypothesis. The central area indicated on Map 1 is the only area where homogeneous Red Cedar exists. The other areas support heterogeneous Red Cedar tending in the direction of an adjacent species. In fact, we owe to this phenomenon of introgression a great many new horticultural varieties of both Red Cedar and Rocky Mountain Juniper. The Platte River type is not pure *J. virginiana* but mixed with *J. scopulorum*. Many of the varieties selected from the Black Hills and other areas by Mr. D. Hill are introgressants. Introgression is an intensifier of variation and seemingly a potent force in speciation.

The question now arises, when and of what duration did the hybridizing occur between Ashe Juniper and Red Cedar? It is inconceivable that it was of recent occurrence, because of the high degree of differentiation in populations and because of the distance from present-day naturally occurring *Juniperus Ashei*. However, it is known that present-day Ashe Juniper occurs along the early-day cattle trails over which Texas herds were transported overland to St. Louis (Parker, 1854). Wolff (1948) states a case of a small juniper plantation developing in the treeless part of Kansas as a result of a cattle drive from Texas. It is possible that even in earlier times buffalo might have dispersed numerous seeds. Likewise, small mammals or birds might have helped these seeds to find a cliff site and become established, sheltered from the alleged frequent fires set by the Indian and white man. From this vantage point, pollen could easily be rained onto the Red Cedar along the creeks, rivers and lesser bluffs. Since promiscuous firing ceased in recent years, the species moved out of the bluffs onto knobs, glades, and ridges, and the introgressant recombinations began to spread to every possible habitat. This, of course, implies a rather terrific rate of migration and ecesis. Even so, these possibilities do not express adequately in terms of time and space the probable generations of back-crossing required to get so complete a spread of the characters of the two species throughout the Ozarks. This hypothesis does not explain the fact that the knobs and glades also represent a whole community of southwestern plants as described in the section on "Ecology."

The most probable interpretation is that mixing in these two species has occurred some time or many times in the past as a result of the climatic fluctuations and consequent floral migrations during and following glacial epochs. The presence of hybrid swarms in restricted areas today is merely a remnant of, or a clue to, the far more extensive migrations and mixings in the past. This hypothesis sheds light on the existence of marked ecotypic differentiation of Red Cedar in the Ozark Highlands, Oklahoma, and Texas. Even today, those fluctuations of climate, which are reflected in the epicycles of erosion in the Southwest (Bryan, 1929, 1940, 1941), probably aid in maintaining the southwestern elements (the present cycle being favorable) on the glades and knobs of the Ozark country, in the absence of repeated burnings. When and if such fluctuations become more severe and consequently more general, they may be sufficient to enlarge the areas in which rates of change characteristic of the Southwest occur.

This may well lead to a marked upset in the balance of things. Such was the case in Pleistocene time.

The historical events discussed above have probably not contributed directly to the structure of the present-day populations of *Juniperus* in periglacial areas. Historical factors, in the geologic sense, probably affect the stabilization of only the most fundamental characters of plant groups, for example, xeromorphism, heliophytism, hydrophytism, and mesophytism. To consider a single historical event, such as isolation in past ages, as the factor responsible for the structure of a modern population or species complex, lumps a great many important processes and events, perhaps more current ones, as impotent forces. It seems more appropriate to consider every force which affects an organism, whether in the Tertiary or yesterday, as an historical factor.

Where introgression is involved, the significance of the historical factor lies in the degree of juggling of germ-plasms made possible through fluctuations in distribution which cause allopatric species to meet. The resultant hybridization enriches the field of variability within the species involved. However, the part of that variability which is subsequently preserved and distributed has little to do with an historical factor in the geologic sense but is determined by the presence and continuity of suitable current habitats.

The final aspect of this work revolves about the question—What is *Juniperus virginiana*? It is, as any field botanist knows, a very complex species which has a distribution befitting a weed. The species has never been fully analyzed and is not likely to be except on a long-term basis. Map 3 illustrates the pattern of differentiation in *J. virginiana* and its geographic relations with other species.

Fassett's (1944, 1945) studies have shown introgression to occur between *Juniperus virginiana* and *J. horizontalis* in the northern states. The pattern of differentiation suggests that hybridization has occurred over a long period of time, since these two species have probably been continuously contiguous since late-glacial time. As a result of Fassett's work and my own field observations, I tentatively set aside area 1-H on Map 3 as the *Northern* geographic race of *Juniperus virginiana*. It is differentiated from *Typica* by having slightly larger fruit, wider and longer whip leaves (12 to 17 mm. long by 1 to 2 mm. wide), longer whip leaf glands (5 to 10 mm.), generally more elliptic, wider spur-leaf glands, a high percentage of curved peduncles, and a high frequency of quadrangular microsporangiate cones. All these characters are in the direction of those of *Juniperus horizontalis*. The habit ranges from var. *crebra* to the typical pyramidal form to var. *ambigens*. On the Coastal Plain of the Atlantic, grotesque forms similar to var. *ambigens* are found, with most of the leafy branches on the offshore sides of the plants. They have coarse whip shoots and long whip leaves with a high frequency of double glands.

The Appalachian Plateaus and the Interior Low Plateaus are the home of the purest Red Cedar, *Typica*, in terms of the amount and extremes of variation and

of the degree to which the populations are free from morphological resemblance to adjacent species. *Typica* and *Ozark* (area 1 and 1-A, respectively, on Map 3) are discussed on previous pages.

On the Gulf Coastal Plain, there is a loose, lax, almost weeping, small-fruited *Florida* race (area 1-B [1-L] on Map 3) which blends into *Juniperus barbadensis*. The relations of this Coastal Plain material, including what is called *J. barbadensis*, to the species of *Juniperus* on the islands in the Caribbean is not at all clear. In the western part of the Coastal Plain as far east as Fort Bulow, Louisiana, there are a few hybrid specimens between *Juniperus virginiana* and *J. Ashei*.

From Fassett's studies of populations from Nebraska northwestward and my studies in western Oklahoma and Texas (Palo Duro Canyon), I designate another geographical race, *Platte River* (area 1-S on Map 3), which may be differentiated from *Typica* by having a high frequency of spur leaf glands close to the leaf tips, a high frequency of non-overlapping spur-leaf tips, slightly larger fruit than *Typica*, long secondary branches with short tertiaries giving a wand-like aspect, acute angle of ascent of the secondary branches giving the aspect of "reaching for the stars." This generally very beautiful race shows modified characters of *Juniperus scopulorum*. These junipers from the Wichita Mountain Wildlife Refuge of southwestern Oklahoma, or the Palo Duro Canyon, Texas panhandle, or the Platte River bluffs of Nebraska, should be prized as seed stock and propagating stock for the high-plains country.

These geographic races are not clearly defined in the sense that each is homogeneous. The species *Juniperus virginiana* is apparently quite youthful, and as a result of introgression from other species it is in the process of becoming polytypic. The fact that junipers are favored in disturbed areas, together with their facility of distribution, inhibits the stabilization of the heterogeneous races. Whether or not these discontinuities ever become absolute is a matter for conjecture.

It seems evident that introgression is probably not a cataclysmic force in evolution but nature's subtle way to bring the elements of the landscape back into some sort of balance during and after change. If climatic change is such that a species migrates and meets a close relative, the habitat at the meeting place may not be very suitable for either species; but through hybridization nature makes new organisms which are actually a product of the change, and some of them will likely be well adapted to the new conditions. Such a process may have widespread effects, but that depends on the distribution of suitable habitats and the efficiency of dispersal of the particular species.

Certainly, introgression is playing a major role in the evolution of *Juniperus virginiana* as an incipient polytypic species. The regions of differentiation shown on Map 3 are rather clearly defined. Because of the tremendous quantities of pollen and seeds produced and the ease with which they are transported over long distances, these population types tend to be swamped by recombining characters; thus the characters do not become stabilized readily, and the boundaries of the elements tend to fluctuate considerably.

SUMMARY

Knowledge of the existence of hybrid swarms between *Juniperus Ashei* and *J. virginiana* led the author to make population studies with the hope of demonstrating the nature and extent of the influence of the two species upon one another. The evidence for hybridization is the character recombinations of the two species in many specimens found where these species grow together.

The comparative morphology of typical members of each species was intensively studied. From the information obtained characters best contrasting the two were selected and used in scoring populations from Virginia and Michigan to Texas. These characters were: ratio of gland length to width, length of typical terminal whip leaf, length of terminal whip at the apex of a typical secondary shoot, length of lateral whip on the same secondary shoot, and percent of decussate spur shoots on the secondary shoot.

These data were converted to pictorialized scatter diagrams so as to integrate the simultaneous variation of several characters. Also, an index was made based on these same characters. A value of 2 was typical for *Juniperus Ashei*, a value of 9.5 for *J. virginiana*. Hybrid swarm mean index values ranged from 3.9 to 6.3, depending on the characteristics of the particular environment and the relative numbers of the two species present.

The index values were plotted on a map to show the geographic distribution of population characters. The results indicate that *Juniperus Ashei* influences *J. virginiana* by introgression throughout the Ozark Plateau and probably as far east as the Tennessee River in the vicinity of the 36th parallel. The reciprocal influence is quite clear but not as common or as extreme. This is undoubtedly because *Juniperus Ashei* has invaded far into the range of *J. virginiana*, while the reciprocal action has not occurred to as great an extent.

A number of hybrid swarms from Missouri to Texas were studied in detail. Glade and bluff junipers in the Ozarks have replicas in those hybrid swarms. This is not true of the glade and bluff junipers of the Interior Low Plateaus.

It is postulated that this introgressive influence was initiated by the fluctuation of the ranges of the two species consequent to climate fluctuation during and following the glacial epochs. Thus, opportunity was afforded these two highly distinctive but sexually compatible species for free hybridization and, especially, for consequent selection of favored back-crosses. The extreme heterogeneity of the junipers of the Ozark Plateau may be explained by this hypothesis. This is obviously a means by which the field of variability of a species may be increased with subsequent changes in ecotypic differentiation through differential selection.

The differentiation of *Juniperus virginiana* as a species is discussed. It embraces five races: (1) *Typica* (the pure species), (2) the *Ozark* (introgressants with *J. Ashei*), (3) the *Platte River* (introgressants with *J. scopulorum*), (4) the *Northern* (introgressants with *J. horizontalis*), and (5) the *Floridan* (introgressants with *J. barbadensis*).

It is postulated that the genus *Juniperus* has evolved along the line of xerophytism, and that *J. virginiana* and *J. barbadensis* have secondarily been selected in the direction of mesophytism. The apparently youthful species *J. virginiana* is in the process of becoming polytypic as a result of introgressive hybridization with four other species. This process is retarded because of the swamping effect of character recombinations as a result of the high efficiency of pollen and seed dispersal and the great numbers of progeny produced. There is little chance for populations to become completely isolated even over great distances.

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EXPLANATION OF PLATE 1

Fig. 1. Seeds of *Juniperus Ashei*: top row, typical plants of the Edwards Plateau; middle and bottom row, from hybrid swarm near Austin, Texas. Scale is in millimeters.

Fig. 2. Seeds of *Juniperus virginiana*: top row, typical plants from Virginia; remaining rows, from hybrid swarm near Austin, Texas.